# Breeding ecology and conservation of the Kentish Plover in Saudi Arabia

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# Breeding ecology and conservation of the Kentish plover in Saudi Arabia

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# Contents

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## Summary

The Kentish plover *Charadrius alexandrinus* is a small ground-nesting shorebird which breeds in temperate and subtropical environments including the Arabian Peninsula. At the Arabian Peninsula ground temperature frequently exceeds the tolerable maxima for eggs and parents, reaching 60°C at midday in summer. Breeding ecology, parental behaviour, distribution and population trends of Kentish plovers in Saudi Arabia are poorly known, and therefore, the first objective of my PhD is to investigate how the extreme hot environment influences their parental care and mating systems. To address this objective, I used video surveillance and transponder systems to record the incubation routines of male and female plovers at their nests over 24 h, and used mixed-effect models to test parental cooperation. I show that ambient temperature has a significant influence on incubation behaviour of both sexes: biparental care – a proxy variable of cooperation between parents – was particularly strong at midday with incubation shared approximately equally between the male and the female (Chapter 2). I suggest parental cooperation is essential to protect the eggs from excessive heat. I experimentally tested this proposition in Chapter 3. Some Kentish plovers nest under bushes and they and their eggs are thus shaded, whereas others nest in the open and are fully exposed to sun. As I expected, the parents coordinate incubation behaviour at exposed nests more precisely than those at covered nests (Chapter 3). In Chapter 4 I investigated the potential impact of the extreme environment on breeding ecology, and show high rates of both mate fidelity and nest-site fidelity, whereas brood desertion was rare - unlike in most other populations that have been studied (Chapter 4). My second objective is to use the Kentish plover as a model species to map spatial distribution in order to identify potential sites that require high conservation priority. To model spatial distribution of plovers I used Generalised Linear Models (GLMs) with four habitat variables derived from remotely-sensed data. I show that Kentish plovers prefer coastal habitats at low elevations, far from settlements, with high soil moisture and low vegetation cover. Based on this model I recommend locations for potential protected areas to be established on the Red Sea coast of Saudi Arabia. I argue that the Kentish plover could be used as a flagship species for designation of new protected areas and thus conservation of Kentish plover habitat will not only protect this species, but will benefit other shorebird species particularly those with similar habitat requirements.

# Chapter 1

# Introduction

Monif AlRashidi

## Parental care

Many organisms provide care for the young. Although some of the best known examples are from vertebrates, care of the young is wide-spread among bugs, beetles, crustaceans and social insects (Clutton-Brock 1991; Tallamy 1999). Three patterns of parental care occur in the animal kingdom: uniparental care by a male or by a female and biparental care by both parents. Biparental care of eggs or young is rare across the animal kingdom but does occur among insects, fishes, amphibians, birds and mammals (Clutton-Brock 1991; Reynolds et al. 2002; McGraw et al. 2010). Biparental care is likely to occur when its presence is crucial to offspring survival, such in harsh environments (Lack 1968; Wilson 1975; Clutton-Brock 1991; Jones et al. 2002; Brown et al. 2010). Experimental removals of one parent usually support this hypothesis, because when one parent was removed the remaining parent was unable (or partly unable) to compensate for the loss of help from its mate (Liker 1995; Gubernick & Teferi 2000; McGuire & Bemis 2007; Houston et al. 2005; Harrison et al. 2009). In addition, biparental care may occur when both parents gain a future benefit from staying together and sharing provisioning, particularly in populations where remating opportunities are low and finding a new mate is difficult (Keenleyside1983; Martin & Cooke 1987; Balshine-Earn & Earn 1998).

Biparental care is a form of cooperation between parents because both the male and the female gain direct reciprocal benefits – high survival of their offspring – by providing care. If one parent lags behind, these benefits may be reduced, or even drop to zero, if the young die. Biparental care, however, also includes conflict, because caring is costly for the parents both in terms of time and energy consumed and in terms of restricted opportunities for future reproduction. Therefore, a sexual conflict over parental care may emerge between parents, since each parent benefits from transferring the burden of care to its partner (sexual conflict over care, Lessells 1999; Arnqvist & Rowe 2005; Houston et al. 2005; Székely et al. 2006; Harrison et al. 2009).

## Incubation behaviour

Incubation behaviour is a major part of parental care particularly in birds and has implications for breeding system evolution (Ligon 1999; Deeming 2002). Incubation is defined as the process of applying optimal temperature necessary for embryonic development to an egg until the egg hatches (Afton & Paulus 1992; Deeming 2002). Four patterns of incubation can be found in birds: 1) biparental incubation whereby both parents incubate the clutch; 2) uniparental incubation where only one parent, the male or the female incubate eggs; 3) communal incubation where more than two birds incubate a single nest; and 4) parasitic incubation, in which intra- or interspecific hosts incubate the clutch (Afton & Paulus 1992; Deeming 2002).

Biparental incubation is the commonest pattern, found in almost 50% of avian families (Afton & Paulus 1992; Deeming 2002). By incubating the eggs, the parents also protect and defend the nest, and by turning over the eggs ensure adequate embryonic development (Deeming 2002). In precocial species, i.e. species in which the parents do not feed their young, incubation is a relatively large part of parental duties (Bergstrom 1986). Incubation is important to regulate the embryonic developmental temperature but it can be costly to the parents because it demands energy. Moreover, incubating birds spend considerable time sitting on the nest, which affects parental fitness and limits their other activities, such as foraging and attracting further mates. Division of incubation duties between parents may reduce the time and energy costs imposed upon any one of them (Deeming 2002).

## Ambient environment and parental care

One of the central ideas in behavioural ecology is that environmental conditions, including food availability, population density, mate availability, weather conditions and predation risk, influence the evolution of mating systems and parental care (Wilson 1975; Clutton-Brock 1991). A good quality habitat may allow a single parent to raise the offspring unassisted which may lead to uniparental care, whereas harsh habitats may require both parents to cooperate to raise their offspring leading to biparental care (Wilson 1975; Clutton-Brock 1991). Ambient temperature is one of the critical environmental variables that influences avian incubation behaviour (Conway and

Martin 2000; Brown and Downs 2003; Amat and Masero 2004). Extreme temperatures (very cold or very hot) may promote more cooperation between parents during incubation because a single parent may be unable to incubate alone and this may increase levels of monogamy.

In most bird species, the optimal temperature for embryo development is between 36ºC and 40.5ºC (Conway and Martin 2000). If ambient temperature deviates from the optimum, parents regulate nest temperature by warming or cooling down the eggs (Webb 1987; Conway and Martin 2000). Extreme temperatures reduce egg survival and have adverse effects on the incubating birds, thus incubating parents have to balance carefully the demands of their eggs with the risk to themselves (Webb 1987). Subsequently, cooperation between both incubating sexes in extremely hot or cold environments may be needed to protect their eggs and themselves from adverse temperatures (Amat and Masero 2004; Tieleman et al. 2008).

## Shorebirds

Shorebirds (sandpipers, plovers, gulls and allies; about 350 species) have a widespread geographic distribution, and can be found on all continents. Studying shorebirds is important from both ecological and conservational points of view (Piersma & Lindström 2004; Stroud et al. 2006; Thomas et al. 2006). Firstly, shorebirds have an outstanding diversity in their life history, behaviour and breeding systems which includes various levels of polygamy by the male or the female (or both sexes), and different levels of care provisioning by the male, female or both parents (Székely et al. 2006; Thomas et al. 2006). Secondly, shorebirds breed in some of the most ostensibly hostile environments on earth: these include cold polar breeding grounds (habitats in the Arctic and Antarctic regions), high mountains, tropical marshes, deserts and semi-deserts (del Hoyo et al. 1996). Therefore, different adaptations are likely to be required to cope with these challenging environments, with potential implications for breeding system evolution.

Finally, this group is an important indicator of global environmental state such as ecosystem health and climate change (Piersma & Lindstrom, 2004; Thomas et al. 2006). Many shorebird populations are declining, and more than half of all shorebird species

are declining globally (International Wader Study Group 2003, Stroud et al. 2006). The reasons for these declines include habitat loss, climate change, pollution, human disturbance and predation.

## Why study Kentish plovers?

The Kentish plover (*Charadrius alexandrinus*) is a widely distributed small shorebird (body mass is 35-45 g) which was thought to have breeding populations on the American, European, Asian and African continents (del Hoyo et al. 1996, Wetlands International 2006). Until recently six subspecies were recognized. Eurasian and African subspecies (*alexandrinus, dealbatus* and *seebohmi*) were called Kentish plovers, whereas three further subspecies in America *nivosus, tenuirostris* and *occidentalis* which have been considered to be part of Kentish plovers were commonly known as snowy plovers (del Hoyo et al. 1996, Wetlands International 2006). However, by comparing genetic and phenotypic characters recently Küpper et al. (2009) provided genetic evidence that the taxonomic status of the Kentish plover and snowy plover needs to be revised, and they should be recognized as separate species. The taxonomic re-evaluation is currently pending, but in this thesis I follow the suggestion of Küpper et al. (2009) and treat Kentish plover as a separate species.

Although Kentish plovers do not approach the threshold for the population decline criterion of the IUCN Red List (BirdLife International 2010), their populations are known to be declining in much of their range. For instance, some European and African populations are declining such as those in Italy, Romania, Hungary, Bulgaria, Sweden Egypt, Mauritania and Guinea-Bissau (Delany et al. 2009), and this species has disappeared as a breeding bird from the British Isles, Norway and in some parts of Spain (Montalvo & Figuerola 2006). Several factors have been identified as contributing to the decline of Kentish plover populations. As for all shorebirds, the major drivers of change are mediated through the transformation, degradation and loss of coastal habitats, disturbance by human activities and predation (Dalakchieva, 2003; Montalvo & Figuerola 2006; Delany et al. 2009; BirdLife International 2010).

Kentish plovers have unusually diverse breeding system (Székely et al. 2006). Both parents incubate the eggs although after the eggs hatch one parent (usually the female)

may desert the family to seek a new mate, so that monogamy, polygyny and polyandry may all occur within a single population (Lessells 1984; Kosztolányi & Székely 2002; Székely et al. 2006). Furthermore, Kentish plover males mainly incubate during the night, whereas females do most of the daylight incubation (Fraga & Amat 1996; Kosztolányi & Székely 2002). However, contribution of males to diurnal incubation appears to be different among populations especially at midday (Rittinghaus 1961, Kosztolányi & Székely 2002; Amat & Masero 2004), presumably because females may not be able to incubate the eggs alone for long period in hot environments (Amat & Masero 2004).

Recent studies suggested that several environmental factors may influence the distribution of care types in Kentish plovers. Biparental care with high parental cooperation is often associated with competition between plover families, high predation risk on chicks and hot ambient temperatures (Székely & Cuthill 1999; Amat & Masero 2004; Kosztolányi et al. 2006). Taken together, this variation in parental care and their tolerance of experimental manipulations make the Kentish plover an ideal species to understand how environmental factors influence the evolution of biparental care and mating system.

## Objectives

My PhD thesis has four specific objectives:

1- To investigate the division of parental effort during biparental incubation in Kentish plovers in extreme hot environments. Ground temperatures in the Arabian Peninsula are often above 50°C at midday during the summer season, and this makes it an ideal site to study the influence of high ambient temperatures on mating systems and parental behaviour of species that breed during this season of the year. I examined how hot temperature influence incubation behaviour of male and female Kentish plovers. I approached incubation from a topical theoretical perspective: conflict and cooperation between individuals. I used data from both day-time and night-time, and mixed-effect models to test parental cooperativeness (Chapter 2).

2- To investigate how nest-site characteristics influence the division of parental effort during incubation. Kentish plovers nest either under bushes or at exposed sites in Farasan Islands, Saudi Arabia. I used data from both day time and night-time, and mixed-effect models to test whether and how nest coverage influences biparental incubation. In addition, I experimentally manipulated nest coverage in both directions (by removing covers from covered nests and covering exposed nests) in the field to test whether exposure to sun influences parental behaviour (Chapter 3).

3- To collect detailed data on behaviour and breeding ecology of Kentish plovers in Saudi Arabia where such these data are largely missing. The only published account of this species reported that it breeds on Farasan Islands and elsewhere in Saudi Arabia, but gave no details. In Chapter 4 I investigated mating system and site fidelity having understood how the hot environment influences incubation (see Chapters 2 & 3).

4- To map suitable habitat and estimate the population size of Kentish plovers along the poorly protected Red sea coast of Saudi Arabia. I combined extensive field surveys, remote sensing, species distribution modelling and distance sampling to address this objective (Chapter 5).

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# Chapter 2

# The influence of a hot environment on parental cooperation of a ground-nesting shorebird, the Kentish plover *Charadrius alexandrinus*

Monif AlRashidi, András Kosztolányi, Clemens Küpper, Innes C. Cuthill, Salim Javed and Tamás Székely

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*Authors' contributions*

**MAR**: statistical analysis, manuscript writing

**AK**: study design, data collection, statistical analysis, comments on manuscript

**CK:** data collection, comments on manuscript

**ICC**: comments on manuscript

**SJ**: comments on manuscript

**TS**: comments on manuscript, general editing

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# The influence of a hot environment on parental cooperation of a ground-nesting shorebird, the Kentish plover *Charadrius alexandrinus*

Monif AlRashidi[1*], András Kosztolányi[2], Clemens Küpper[1], Innes C Cuthill[3], Salim Javed[4], Tamás Székely[1]

## Abstract

**Background:** Parental care often increases offspring survival, but is costly to the parents. A trade-off between the cost and benefit of care is expected, so that when care provisioning by both parents is essential for the success of young, for instance in extremely cold or hot environments, the parents should rear their young together. We investigated the latter hypothesis in a ground nesting shorebird, the Kentish plover *Charadrius alexandrinus* in an extremely hot environment, the Arabian Desert. Midday ground temperature was often above 50°C in our study site in Abu Dhabi (United Arab Emirates), thus leaving the eggs unattended even for a few minute risks overheating and death of embryos.

**Results:** Through the use of video surveillance systems we recorded incubation routines of male and female Kentish plovers at 28 nests over a full day (24 h). We show that ambient temperature had a significant influence on incubation behaviour of both sexes, and the relationships are often non-linear. Coordinated incubation between parents was particularly strong in midday with incubation shared approximately equally between the male and the female. The enhanced biparental incubation was due to males increasing their nest attendance with ambient temperature.

**Conclusions:** Our results suggest biparental care is essential during incubation in the Kentish plover in extremely hot environments. Shared incubation may also help the parents to cope with heat stress themselves: they can relieve each other frequently from incubation duties. We suggest that once the eggs have hatched the risks associated with hot temperature are reduced: the chicks become mobile, and they gradually develop thermoregulation. When biparental care of young is no longer essential one parent may desert the family. The relaxed demand of the offspring may contribute to the diverse breeding systems exhibited by many shorebirds.

## Background

Biparental care of eggs or young is uncommon in the animal kingdom although it does occur among insects, fishes, amphibians, birds and mammals [1-4]. Biparental care, however, is a common behaviour in certain groups of animals: for instance 40% of cichlid fish genera and 32% of primate species are biparental [5]. These species provide excellent opportunities to investigate *how* and *why* biparental care evolves, and to tease apart the roles of parental investment, sexual selection and conflicts in breeding system evolution [*sensu*-[6-9]].

Two major groups of hypotheses have been proposed to explain biparental care [reviewed by [2,10,4]]. On the one hand, both parents may be essential for successful rearing of the young; the parents may need to share incubation, brood defence or protection of the territory in order for the young to survive [11,12]. Biparental care may be essential if parents breed in resource poor environments, or the physical environment is harsh and challenging [13]. Experimental removal of one parent (usually, the male) supports the hypothesis that biparental care provides direct benefits by enhancing offspring survival, and/or by putting less strain on the female [2,14-17]. On the other hand, parents may benefit in future from staying together and sharing care provisioning [18]; for instance by keeping their partner for future

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matings and therefore avoiding the costs related to finding/attracting a new mate. Staying with the mate and helping him/her might be particularly beneficial if there are few opportunities for finding a new mate [4].

Biparental care is particularly common among birds: approximately 50% of bird species have biparental incubation and/or brood care [11,12,19,20]. Although in these species the parents cooperate to rear the young, there are also elements of conflict because the benefit of care, i.e. the offspring, is shared between biological parents whereas each parent pays the cost of care itself. Therefore each parent prefers the other to invest more resources in rearing the young [sexual conflict over care [21,22,7,23]].

Incubation is essential for successful reproduction in nearly all bird species, because eggs require heat for embryonic development, and the incubating parent can defend the clutch from potential predators [24,19]. However, incubation can be costly to the parents because it demands time and energy, and the incubating parents themselves become exposed to predators [25,26]. By sharing incubation, the parents reduce the costs of time, energy and predation risk imposed upon them [19].

The optimal temperature for embryo development in most birds is between 36°C and 40.5°C, and if ambient temperature deviates from the optimum, parents regulate nest temperature by warming or cooling the eggs [27,28]. Overheating and chilling (hyper- or hypothermia, respectively) reduce egg survival and may cause nest failure. Hyperthermia is more harmful than hypothermia, since hot temperatures induce embryonic mortality faster than cold ones; embryos may survive 0° C for a short time period, whereas no avian embryo survives above 44°C [27]. Therefore parental care in hot environments, especially of ground-nesting birds where the eggs might be directly exposed to the heat of the sun, plays a vital role in preventing eggs from overheating [29,30].

We investigated parental cooperation - defined here as mutually beneficial interactions between the parents to maximise their reproductive success [31] - in a small cosmopolitan ground-nesting shorebird, the Kentish plover, *Charadrius alexandrinus* (body mass approximately 42 g), which breeds in temperate and subtropical environments [32-34]. Nests are sparsely filled with material such as straw, pebbles, mollusc shells and algae which may act as insulation materials to help regulate egg temperature [32,35]. Both parents participate in incubation: females usually incubate in the daytime whereas males incubate during night [36,37], although after hatching of the eggs one parent (usually the female) may desert the brood. The Kentish plover is an ideal species for studying parental behaviour, since it has variable parental care both within and between populations. Monogamy, polygyny and polyandry may all occur along with male-only, female-only and biparental brood care within a single population [38-41]. All three types of brood care that occur in Kentish plovers were recorded in the Arabian Desert, although biparental care of young appears more common than in temperate zone populations such as Hungary and France [42]. The transition from biparental incubation to biparental/uniparental brood care is an excellent paradigm to understand how and why animals shift from biparental care to uniparental one.

Here we investigate the division of parental effort during biparental incubation in Kentish plovers in the Arabian Peninsula where ground temperatures may exceed 60°C at midday during the breeding season. The objectives of our study were to answer two questions: i) Is the behaviour of the male or the female influenced by ambient temperature? ii) Does ambient temperature influence parental cooperation during incubation? We predicted that (i) male contribution to incubation should increase with ambient temperature to assist female incubation, and (ii) total incubation will increase with ambient temperature, so that parental coordination will be tight during the hottest part of the day.

## Methods

### Study area

Fieldwork was carried out in Al Wathba Wetland Reserve between 13$^{th}$ of March and 23$^{rd}$ of July 2005, and between 26$^{th}$ of April and 12$^{th}$ of July 2006. This reserve is located approximately 40 km south-east of Abu Dhabi in the United Arab Emirates (24° 15.5' N, 54° 36.2' E). The fenced reserve with a total size of about 465 ha is composed of artificially created water bodies that are surrounded by sand dunes. About 200 pairs of Kentish plover breed within and around the reserve [42].

### Data collection

Kentish plovers are sexually dimorphic during the breeding season which allows identification of sexes from photos [43]; adult males have black eye-stripes; black frontal head bars and incomplete black breast-bands, whereas these areas are pale brown in adult females. Sexual dimorphism in plumage fades over the season, therefore at four nests in 2005 the eye and head stripe of males were dyed using black permanent marker to facilitate discrimination between males and females from the nest photos.

Activities at the nests were recorded using a small spy camera (Outdoorcam, Swann Communications Pty. Ltd.) positioned about 1 m from the nest [44]. The camera was connected to a digital video recorder (Memo-Cam, Video Domain Technologies Ltd.) that recorded an image every 20 s. The camera was equipped with

infrared lights to capture the images of incubating plovers during night. Power was supplied by a car battery (12 V). All parts of the system (except the camera), and the cables were hidden underground to minimize the disturbance to the birds. The ambient temperature was measured by a thermo-probe which was placed about 25 cm from the nest scrape at ground level. The probe was connected to a data logger (Tinytag, Gemini Data Loggers Ltd.) that recorded the temperature every 20 s. Ground temperature often exceeded 50°C at midday (Fig. 1); the maximum ground temperature recorded was 64.8°C.

To control for seasonal changes, we noted egg-laying date (the date of the last egg laid in the clutch) or estimated it by floating eggs in lukewarm water [45]. Egg-laying was then calculated as the number of days between 1 March and egg-laying date.

Ambivalent identification of male and female, and records when the parents were disturbed (e.g. during daily function tests of the data recording systems) were excluded from analyses (< 2.3% of all records). At 11 nests data between 22:00 h and 24:00 h were not used in the current analyses, because these nests were manipulated after 22:00 h [see [44]]. In total, data from 28 nests (20 and 8 nests from 2005 and 2006, respectively) were included in the analyses.

### Statistical procedures

Daily 24 h recordings starting at midnight (0.00 h) were considered as the unit of analysis. Each day was divided into twelve 2 h time periods. Five behavioural variables were calculated for each interval: (1) *total incubation*, the percentage of time when the eggs were incubated by either parent; (2) *male incubation*, the percentage of time when the eggs were incubated by the male, (3) *female incubation*, the percentage of time when the clutch was incubated by the female, (4) *changeovers*, the number of cases when one parent was relieved by the other parent, (5) *length of off-nest periods*, the mean of off-nest periods that began in the given interval. For variables (1)-(3) an equivalent terminology would be 'nest attentiveness', although to be consistent with our previous studies we prefer to use the term incubation [46]. Note that by incubation we mean keeping the egg temperatures close to the optimal temperature for embryonic development, and thus it includes both keeping the eggs warm and shading them for excessive ambient heat. Proportion variables were arcsine square-root transformed for normality. Changeovers and length of off-nest periods were $\ln(x + 1)$ transformed for normality. The average ground temperature measured during each period was taken as the ambient temperature.

The influence of ambient temperature on incubation behaviour was investigated using linear mixed-effects models [47] with nest identity as a random factor, since parental behaviour is not independent between two-hour time periods for a given nest. Year, egg laying date and nest age (i.e. the number of days since the start of incubation) potentially influence incubation behaviour. We tested all three covariates on our response variables (total incubation, male incubation, female incubation, changeovers, length of off-nest periods), and the only significant effect was a difference in length of off-nest periods between years (mixed-effects models $P = 0.020$, all other $P \geq 0.060$), therefore these variables were not included in further analyses. However, for length of off-nest periods we checked that our conclusion does not change if we include the significant year effect in the final model (Table 1).

The initial models of total incubation, changeovers and length of off-nest periods included time period as a fixed factor and ambient temperature as second degree orthogonal polynomial covariate because avian incubation behaviour and ambient temperature are not linearly associated [28], and the interaction term between time period and ambient temperature. Our initial model for male and female incubation included time period (fixed factor), ambient temperature (second degree orthogonal polynomial covariate), the incubation by the other sex (covariate) and all second-order interactions. All models included a random intercept term for each nest. The initial models were fitted using maximum likelihood method, and model selection was carried out using the function stepAIC [48]. The final models were refitted using restricted maximum likelihood (Table 1).

We checked whether the effects of temperature and temperature$^2$ on incubation behaviour is due to within-subject or between-subject effects using within-group centering [49,50], and concluded that there is no difference between the within-subject and between-subject effects in any of the response variables ($P > 0.3$). Therefore our results from mixed-effects models reflect the within-subject effects.

We illustrate the results of the final mixed-effects models on S1-S3 (additional files 1, 2, 3) by fitting mixed-effects models of the variables showed in the figures, and present the back-transformed fitted values and the observed data. We used R version 2.7.1. and 2.8.1. for statistical analyses. Values are given as mean ± SE unless stated otherwise.

## Results

### Daily routine

Overall, the mean total incubation was 85.7 ± 1.1% over the full day (n = 28 nests). Females attended the nest 44.5 ± 1.7% of time, whereas males attended the nest 41.3 ± 1.6% of time. Male and female incubation routines were different: females incubated the eggs mostly in morning and males in the evening and at night (Fig.

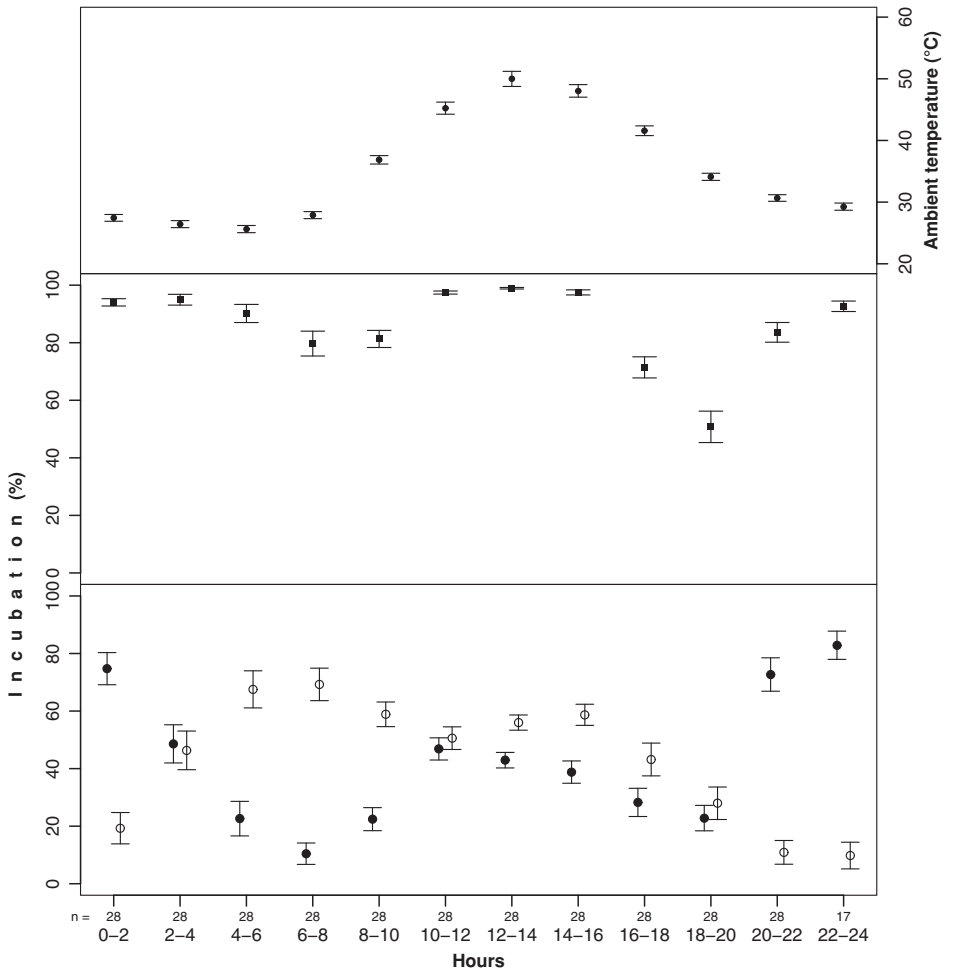


**Figure 1** Ambient temperature (top panel), and incubation by male (filled circles), female (opened circles) and both parents (filled squares) at Kentish plover nests in Abu Dhabi (mean ± SE for each two-hour time period, n is the number of nests used in the analyses).

**Table 1 Final mixed-effects models of incubation behaviour in the Kentish plover (Type III SS ANOVA).**

| Explanatory variables | Response variable | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | % total incubation $df_{error}$ = 262 | | | % male incubation $df_{error}$ = 250 | | | % female incubation $df_{error}$ = 261 | | | Changeovers $df_{error}$ = 262 | | | Length of off-nest periods $df_{error}$ = 208 | | |
| | df | *F* | *P* | df | *F* | *P* | df | *F* | *P* | df | *F* | *P* | df | *F* (*F*) | *P* (*P*) |
| Time period | 11 | 1.44 | 0.157 | *11* | *2.61* | *0.004* | 11 | 0.81 | 0.632 | 11 | 1.138 | 0.332 | *11* | *1.980 (2.019)* | *0.032 (0.028)* |
| Ambient temperature | 2 | 0.25 | 0.782 | 2 | 0.35 | 0.704 | 2 | 0.75 | 0.475 | 2 | 0.856 | 0.426 | 2 | 0.877 (0.773) | 0.418 (0.463) |
| Female incubation | | | | *1* | *118.21* | *<0.001* | | | | | | | | | |
| Male incubation | | | | | | | *1* | *614.79* | *<0.001* | | | | | | |
| Time period × ambient temperature | *22* | *3.25* | *<0.001* | *22* | *2.95* | *<0.001* | *22* | *2.51* | *<0.001* | *22* | *1.971* | *0.007* | *22* | *1.744 (1.733)* | *0.024 (0.026)* |
| Time period × female incubation | | | | *11* | *3.36* | *<0.001* | | | | | | | | | |

Ambient temperature was included in the models as second degree orthogonal polynomial. Statistically significant terms are in italics. *F* and *P* values in parentheses are taken from the alternative model that included also the significant ($P = 0.037$) year effect.

1). At night (20:00 - 6:00 h) total incubation was 90.8 ± 1.4%, with females and males spending 33.2 ± 3.6% and 57.6 ± 3.6% of their time respectively. In contrast, during daytime (6:00 - 20:00 h) the nests were attended 82.4 ± 1.4% of the time, with females and males attending 52.1 ± 2.1% and 30.4 ± 1.8% of their time respectively. The nest was attended by either parent over 70% of time in each period except 18.00-20.00 h, and the highest attendance was during midday (Fig. 1).

### The influence of ambient temperature on incubation

Ambient temperature influenced incubation behaviour as with increasing temperature the parents changed over incubation more frequently (Fig. 2, Table 1), and the length of off-nest periods were reduced (Fig. 3, Table 1).

The effects of ambient temperature on incubation, however, were often not linear (Fig. S1-S3, additional files 1, 2, 3, Table 1). In the morning as ambient temperature increased, total incubation decreased with temperature. In midday, however, total incubation increased with temperature (Fig. S1, additional file 1). In late evening, total incubation decreased again with temperature.

Males and females responded differentially to ambient temperature during different parts of the day, as indicated by the highly significant interaction terms between time period and temperature (Table 1). During midday males usually increased incubation with temperature, whereas females decreased (Figs. S2-S3, additional files 2, 3).

### The influence of ambient temperature on parental coordination

Female and male incubation tended to show a trade-off, and the strength of this relationship varied significantly over the day (Table 1, Fig. 4). In the morning (6:00 -

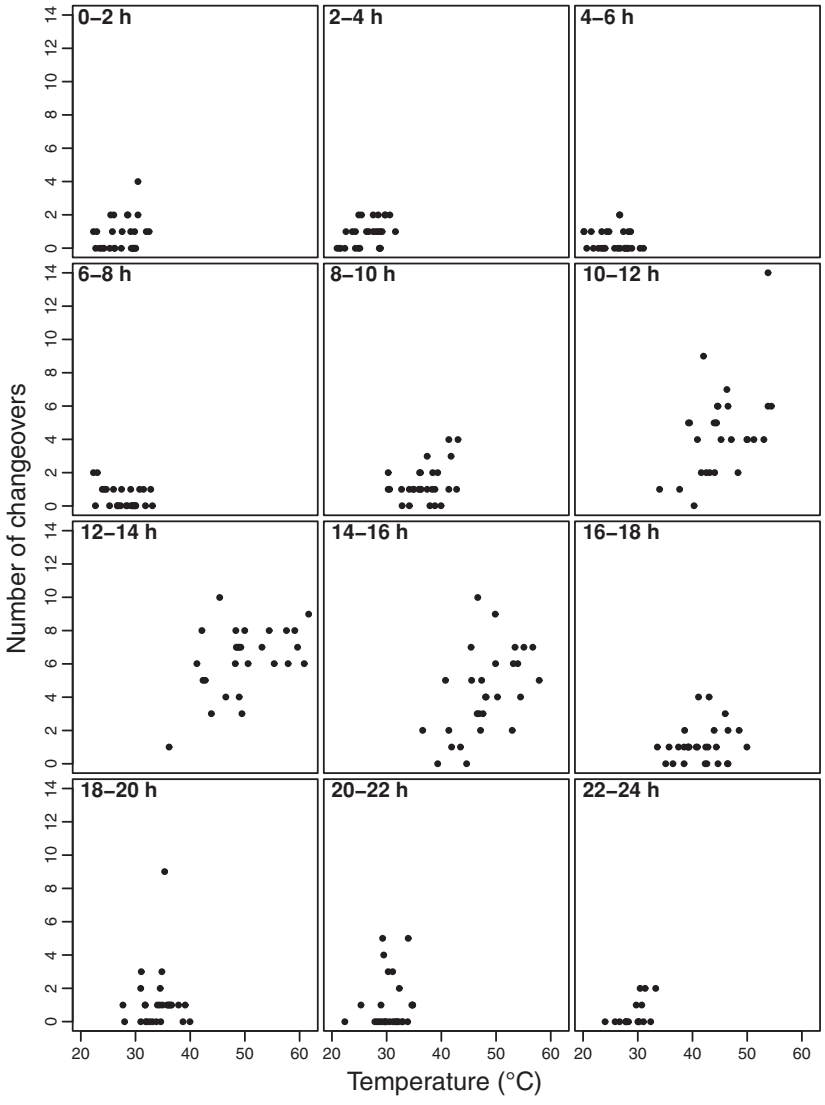


**Figure 2 Number of changeovers in relation to ambient temperature (°C)**.

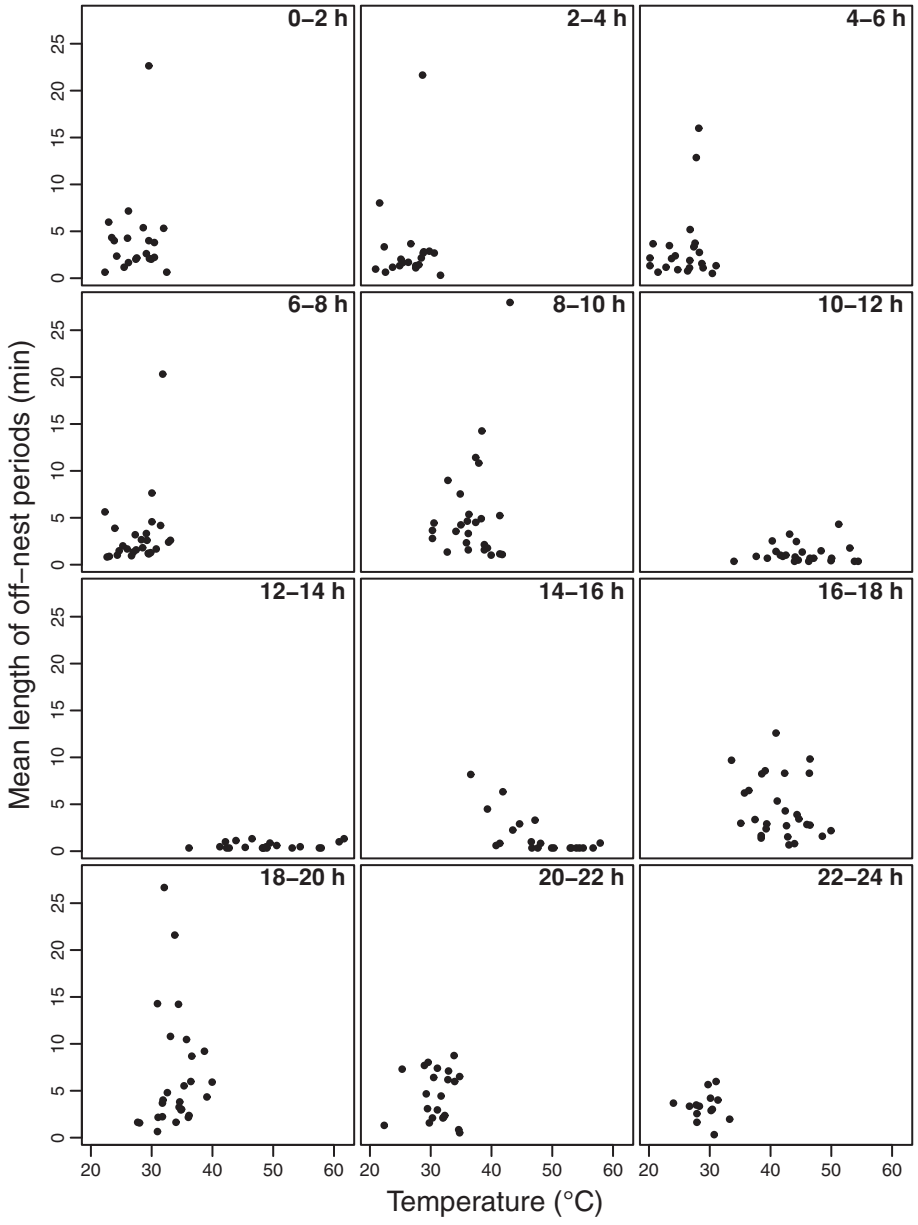


**Figure 3 Length of off-nest periods (mean length, in minutes) in relation to ambient temperature (°C)**.

10:00 h) and in the evening (16:00 - 20:00 h) the inverse relationship between male and female incubation was poor. In contrast, during midday (10:00 - 14:00 h) the parents practically covered the nest continuously, and at most of the nests incubation was split approximately half between the male and the female (see also Fig. 1).

## Discussion

Our study provided two major results. Firstly, ambient temperature had a significant influence on incubation behaviour; the relationship was non-linear and depended on the time of the day. This suggests a complex relationship between incubation, ambient environment and time of the day. Incubation behaviour is expected to decrease with ambient temperatures until it reaches the optimal egg temperature and increase above the optimal egg temperature. However, as Figs S2-S3 (additional files 2, 3) suggest, there are many deviations from this pattern. The high resolution of our data taken over a full day, and *a priori* inclusion of time and ambient temperature effects, allowed us to reveal patterns that vary between different times of the day.

Secondly, understanding how a single parent responds to changing ambient conditions is not satisfactory,

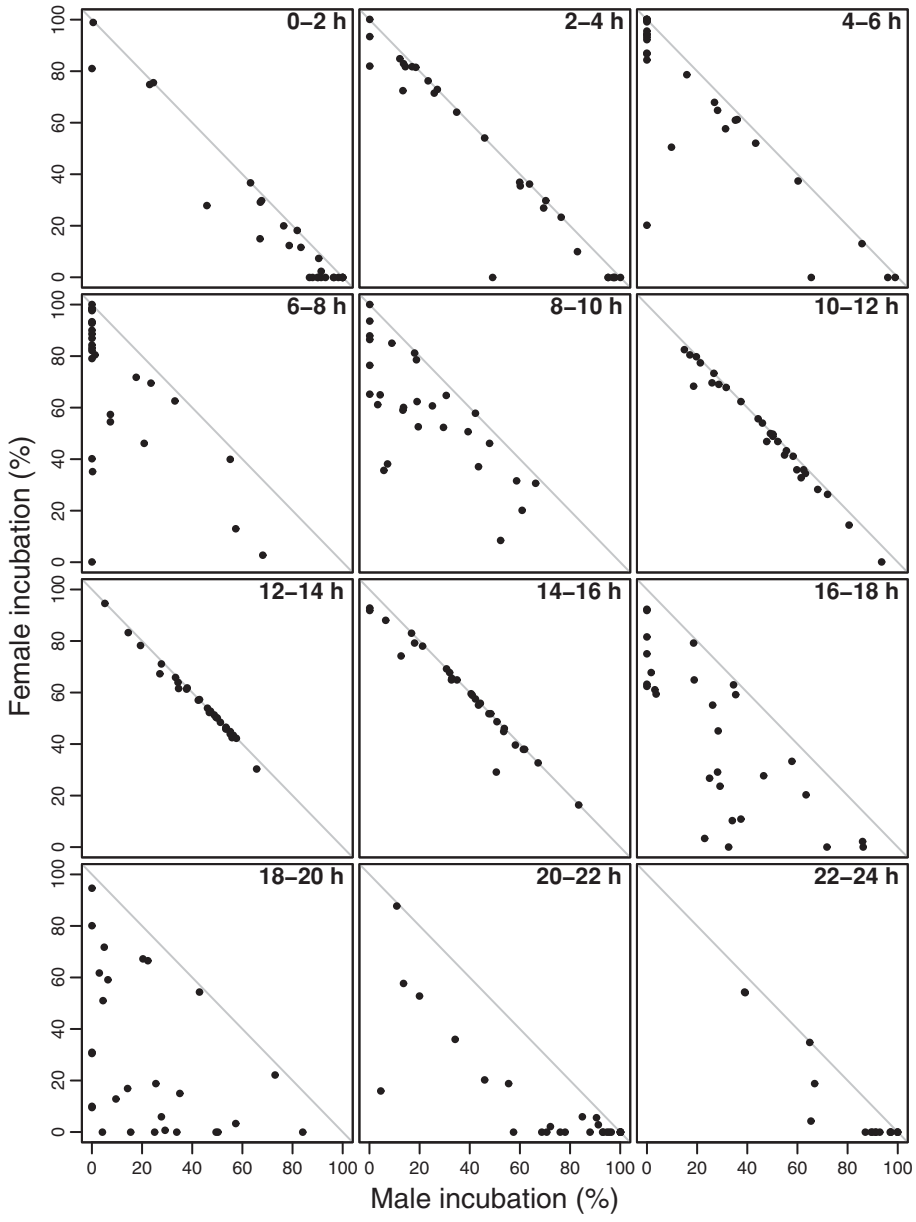


**Figure 4 Female incubation (%) and male incubation (%) in two-hour periods**. The grey line (-1 slope) shows the 100% total incubation threshold.

because in shared incubation systems the behaviour of a parent is influenced by the behaviour of its mate [51]. This is illustrated by the reversed response of males and females to ambient temperature during midday: male incubation tended to increase with temperature whereas female incubation was tended to decrease. In addition, the extreme temperature has important implications on parental coordination since parents showed tighter coupling in their incubation behaviour at high daytime temperature by sharing incubation equally and increasing number of changeovers. Following this strategy helps the parents coping with heat stress; they can relieve each other frequently from incubation duties.

Our results are in line with those of Purdue [32] who reported that nest attendance in the snowy plover *Charadrius alexandrinus nivosus* increased during hot parts of the day and off-nest periods were reduced. In late afternoon, however, nest attendance decreased, possibly because the latter period was suitable for foraging, and ambient temperature did not harm the embryos in the unattended eggs. Our results are consistent with the work of Amat and Masero [34] who suggested that hot

ambient temperature may limit the length of incubation bouts, since females cannot sustain incubation for long periods. Hence increased incubation by the male in midday appears to assist the female in taking short time periods off the nest. However, we believe that our study goes beyond previous studies and is novel for several reasons. First, we used longer continuous records (24 h) and larger sample sizes. Second, we used linear mixed-effects models to control for non-independence between time periods, and statistically control for the effect of the other sex whilst investigating ambient temperature on the behaviour of the focal parent. Since incubation behaviour is usually not linearly associated with ambient temperature [28], we also use a quadratic term in our models. Finally, our conceptual framework was to understand how ambient environment influences biparental cooperation, whereas the focus of previous studies was the ability of a single parent to cope with heat stress.

An alternative explanation for the highly coordinated pattern of incubation is complex interactions (or negotiations) between parents [52] and coercion; for instance one parent may coerce the other to work harder. From the still images we took at the nests we cannot infer coercion, so that additional observational or experimental data are required to determine whether the female drives the precise timing of changeovers. However, we argue female coercion is unlikely. Male and female plovers have similar body sizes, and both sexes are well equipped for fighting [53]. In addition, coercion tends to be a trait of the behaviourally dominant sex, in this case, the male.

Results of our study are important for three reasons. Firstly, they suggest that at extreme hot temperature cooperation between the male and female parents is essential to raise the young. Parental behaviours, including incubation, provide good model systems to understand how two, usually unrelated, individuals cooperate in nature, given that the survival of their young often depends on care provisioning by both parents [7,4]. Secondly, incubation of ground-nesting birds puts the adults under severe heat stress in deserts, and interrupting incubation for more than a few minutes would kill the embryos [34]. These conditions should favour tight cooperation; the adults thereby reduce risk both to themselves and to their eggs. Males may be forced (in evolutionary time) to participate in daytime incubation, because females cannot manage the task alone. Therefore, extreme temperatures may increase the level of parental cooperation, and reduce sexual conflict over care [this study, [34]].

Thirdly, once the eggs have hatched the risks associated with high ambient temperature are reduced, since the chicks become mobile, and both the adults and their young can better regulate their body temperature, for instance by bathing more frequently or by moving under shade. Since chicks require a diminishing amount of protection, shading and attendance from their parents [23], desertion by one of the parents becomes less costly. Nevertheless, biparental care and parental cooperation may still be favoured by certain environmental variables such as localised food distribution and high predation on the chicks. For instance, when food distribution was patchy but abundant, the density of plovers increased and competition between families intensified [53], the parents spent more time defending their young and an extended biparental brood care was observed. In another study, Fraga and Amat [36] noted that long biparental care was a response to heavy chick predation in Kentish plovers by gull-billed terns *Sterna nilotica*, whereby protection by both parents were likely more effective than by a single parent.

## Conclusions

Our results suggest that extremely hot environment favours cooperation between incubating Kentish plover parents. The increased parental cooperation is essential, since a single parent cannot protect the eggs and/or itself from overheating. Experimental analyses of male-female interactions, and comparing the incubation responses of males and females across different plover populations are important avenues for revealing the complex relationships between ambient environment, parental cooperation and sexual conflict.

**Additional file 1: Fig. S1** Total incubation (%) in relation to ambient temperature (°C) in two-hour periods: observed (filled circles) and fitted values (asterisks) are shown from mixed-effects model (see Methods for details).
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**Additional file 2: Fig. S2** Male incubation (%) in relation to ambient temperature (°C) in two-hour periods: observed (filled circles) and fitted values (asterisks) are shown from mixed-effects model (see Methods for details).
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[ http://www.biomedcentral.com/content/supplementary/1742-9994-7-1-S2.EPS ]

**Additional file 3: Fig. S3** Female incubation (%) in relation to ambient temperature (°C) in two-hour periods: observed (filled circles) and fitted values (asterisks) are shown from mixed-effects model (see Methods for details).
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**Authors' contributions**
ICC and TS conceived the study, and together with AK designed the project. Fieldwork was carried out by AK and CK. SJ provided the permissions and logistics. Statistical analyses were carried out by MAR and AK, and writing up was lead by MAR. The manuscript received inputs from all co-authors. All authors read and approved the final manuscript.

**Competing interests**
The authors declare that they have no competing interests.

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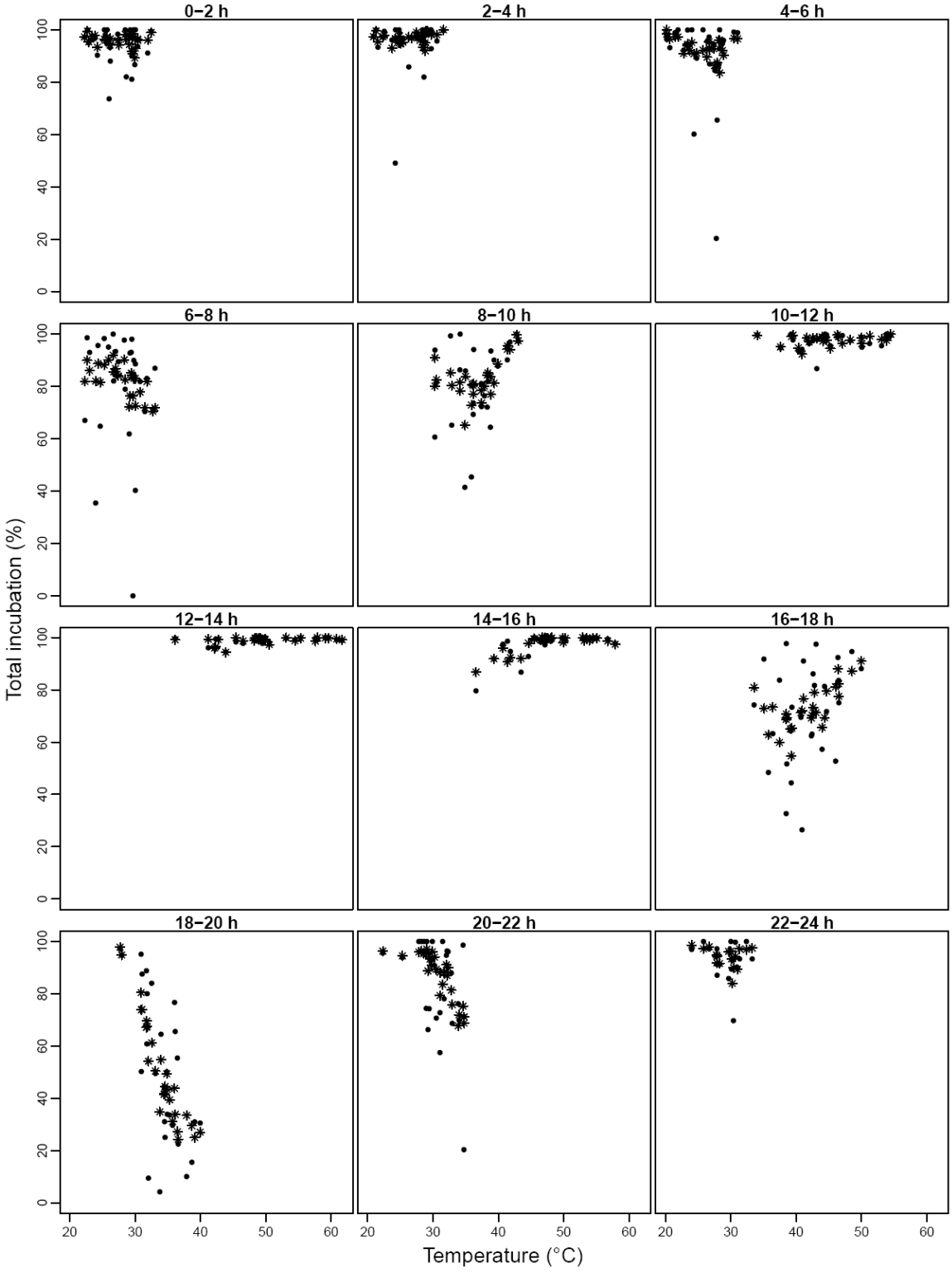
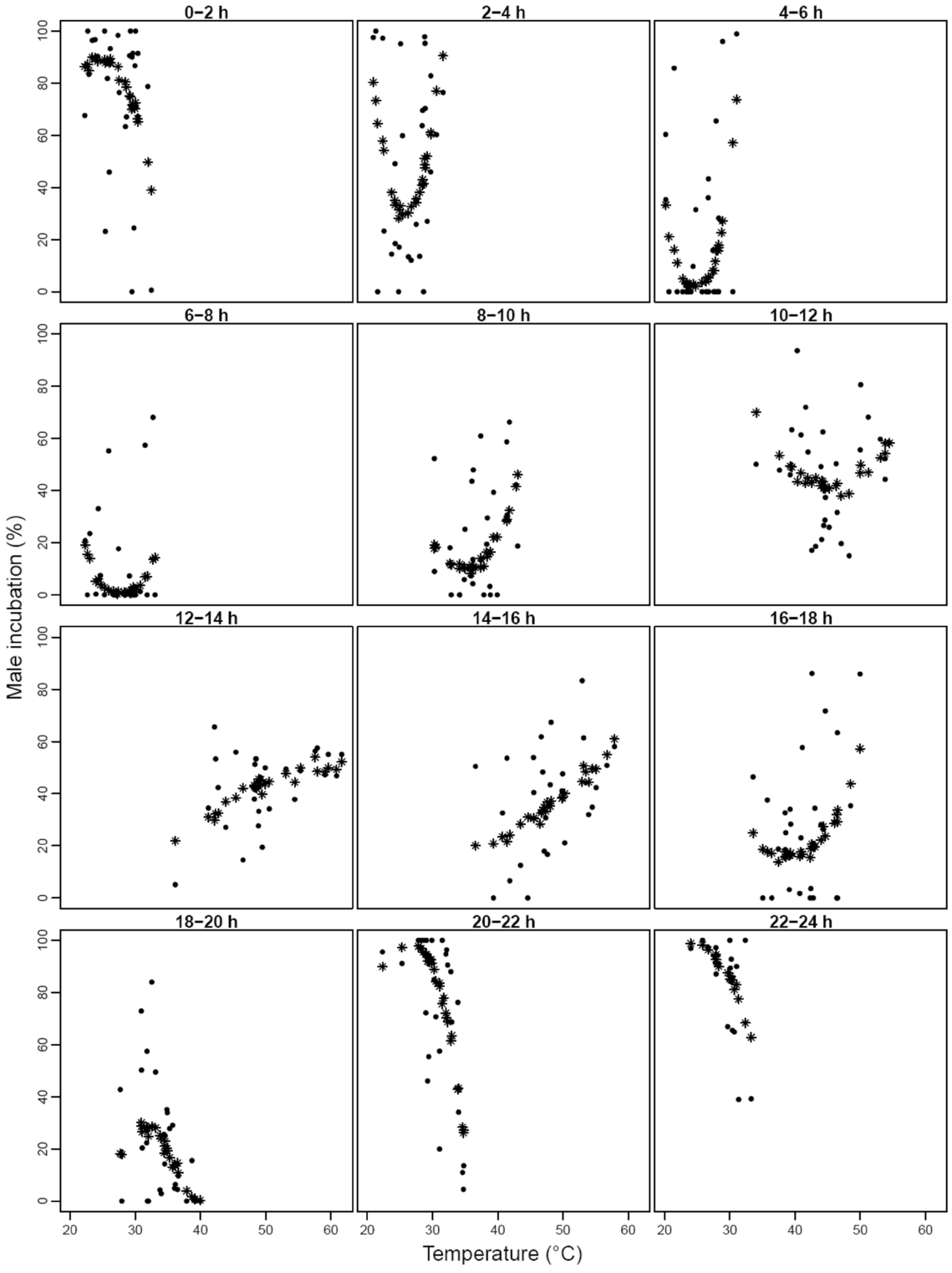
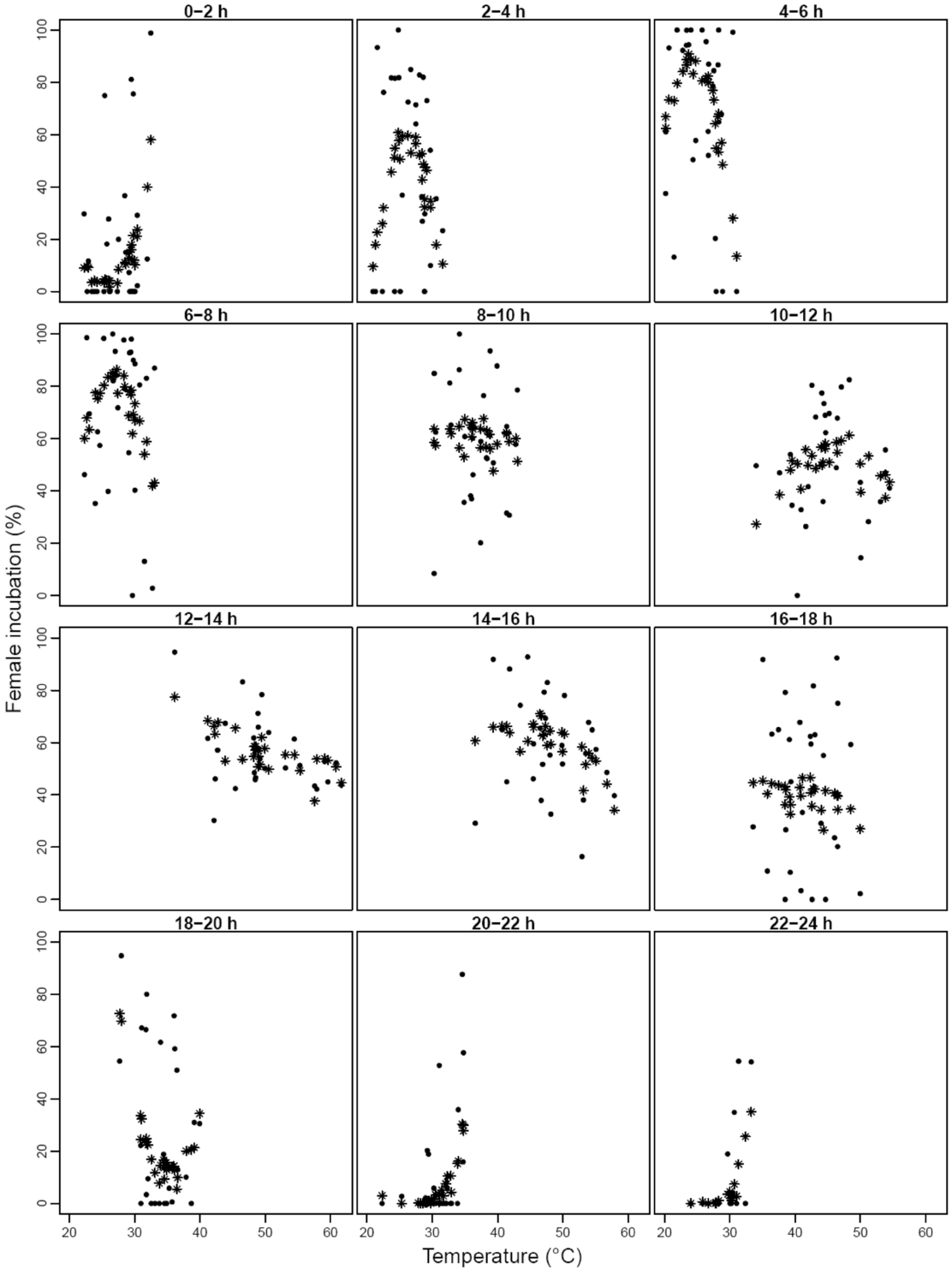



Additional file 1.Total incubation (%) in relation to ambient temperature (°C) in two-hour periods: observed (filled circles) and fitted values (asterisks) are shown from mixed-effects model (see Methods for details).




Additional file 2. Male incubation (%) in relation to ambient temperature (°C) in two-hour periods: observed (filled circles) and fitted values (asterisks) are shown from mixed-effects model (see Methods for details).




Additional file 3. Female incubation (%) in relation to ambient temperature (°C) in two-hour periods: observed (filled circles) and fitted values (asterisks) are shown from mixed-effects model (see Methods for details).

# Chapter 3

# The effect of nest-cover on biparental incubation of Kentish plovers in an extreme hot environment

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*Manuscript*

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**MAR**: data collection, statistical analysis, manuscript writing

**AK**: statistical analysis, comments on manuscript

CK: comments on manuscript

**MS**: comments on manuscript

**TS**: comments on manuscript, general editing

## Abstract

Harsh environments are expected to influence parental behaviour, although experimental evidence is scanty given the difficulty in manipulating environmental conditions in nature. We manipulated nest cover in the Kentish plover *Charadrius alexandrinus,* a ground-nesting shorebird breeding on Farasan Islands, Saudi Arabia. In this small bird both parents incubate the nest, and previously we showed that the parents incubate the eggs most intensively and coordinate nest changeovers during the hottest part of the day. Here we exploit the natural variation in nest cover to test how reduced (or enhanced) exposure to the sun influences the incubation behaviour of male and female plovers. This experiment is especially relevant in harsh environment, such as our study site in Saudi Arabia, where ground temperatures are usually above 50°C at midday. We found that at naturally exposed nests the parents spent more time incubating the eggs, and they changed over incubation bouts more often than at covered nests. Experimental manipulations of nest cover provided consistent results: parents at experimentally exposed nests increased incubation effort, and they changed over incubation roles more frequently than at experimentally covered nests. We conclude that exposure to solar radiation has a major influence on biparental incubation in the Kentish plover, and this conclusion is consistent with the proposition that harsh environments select for biparental care.

## Introduction

In the animal kingdom, parental care is an extremely variable social trait both within and between species and can be correlated with variations in physiological constraints and ecology (Clutton-Brock 1991; Krebs & Davies 1993). On the one hand, species exhibit large variation in the forms of care they provide (e.g. guarding and incubating eggs in birds and gestating and suckling neonates in mammals) (Clutton-Brock 1991). On the other hand, the number and sex of care-giving parent are also variable: in many invertebrates, reptiles and mammals the female is the sole care provider, in fishes parental care is largely provided by the male, whereas in birds and certain groups of mammals (e.g. primates, carnivores) and fish, (Cichlid fishes) biparental care is common (Clutton-Brock 1991, Tallamy 1999; Reynolds et al. 2002).

An oft-cited, yet rarely tested hypothesis is that environmental harshness can select for biparental care. Under harsh environmental conditions biparental care is essential for offspring survival, since a single parent may be unable to protect the offspring and/or itself from hostile conditions (harsh environment hypothesis, Lack 1968; Wilson 1975; Jones et al. 2002). Few studies have highlighted the fact that several environmental factors can influence biparental care in animal species. Extreme weather conditions, food scarcity, competition between neighbours and high predation risk on offspring can all select for enhanced biparental care (Wynne-Edwards 1998; Kosztolányi et al. 2006; Amat et al. 2008; Tieleman et al. 2008; Brown et al. 2010).

All these previous studies were observational except the study of Brown et al. (2010) which used both observational and experimental approaches because manipulation of environmental harshness in nature is extremely challenging work. In this study, we tested the harsh environment hypothesis using the Kentish plover *Charadrius alexandrinus* a small ground-nesting shorebird, as a model species. The Kentish plover is an ideal species for testing this hypothesis since both sexes incubate the eggs, and ambient temperature predicts incubation behaviour (Amat & Masero 2004a; AlRashidi et al. 2010). Previously we showed that ambient temperature and time of the day predicts total incubation, male incubation, female incubation and the number of changeovers (AlRashidi et al. 2010). However, these results are correlational and to establish the effects of ambient environment require experimental testing. The natural variation in nest cover offered an excellent opportunity to carry out such an experiment,

since in the Farasan Islands, Saudi Arabia, some nests are covered by halophytic bushes whereas many others are open to solar radiation and not covered (see Results). By manipulating nest cover we aimed to test the harsh environment hypothesis. The ground temperatures at our site were usually above 50°C at midday.

The objectives of our study were to: 1) test whether exposure to the sun may influence incubation behaviour of male, female or both parents. We predicted that nesting at exposed sites enhances parental cooperation in comparison with covered sites because of increased temperatures. The harsher conditions at exposed sites will lead to more frequent changeovers of attending parents especially during midday. 2) We experimentally manipulated nest cover (increased or decreased), and expected that at experimentally exposed nests the parents will increase their incubation effort and make more frequent nest changeovers, whereas at experimentally covered nests we expected the opposite pattern.

## Methods

### *Study area*

Fieldwork was carried out between 17$^{th}$ of April and 4$^{th}$ of July 2008, and 15$^{th}$ of May and 4$^{th}$ of July 2009 in Farasan Island, the largest island of the Farasan Island archipelago that is located in the Red Sea about 50km from the city of Jizan, Saudi Arabia. The archipelago is a protected area established in 1996 by Saudi Wildlife Commission (SWC), and covers an area of 3,310 km$^2$ (PERSGA/GEF, 2003). Farasan Islands have a subtropical desert climate and rainfall is sparse and the average annual precipitation is less than 50 mm, but being surrounded by the sea, humidity is high all year round (NCWCD 2000). Vegetation is dominated by halophyte plant species such as *Halopeplis perfoliata, Zygophyllum album, Zygophyllum coccineum, Zygophyllum simplex, Limonium axillare, Suaeda monoica*. The degree of grazing pressure by wild Farasan Island gazelles *Gazella gazella farasani* and domestic herds (e.g. goats and camels) is minor, thus these plant species are abundant, covering a huge area of salt marsh and sand dunes and providing nesting sites for breeding shorebirds (NCWCD 2000).

***Fieldwork methods***

Kentish plovers nest sparsely up to 1 km away from the shore under halophyte bushes or in exposed sites. Two methods were used to locate nests, by driving a car at slow speed and flushing the incubating birds or by watching incubating birds when they expressed belly-soaking behaviour between 10.00 h and 15.00 h (local time, GMT + 3 hours) and following these parents back to their nests. Once a nest was found, we recorded the size of the clutch, photographed the nest and determined its geographic coordinates using a hand held GPS unit. Nests were allocated to five cover categories: completely exposed nests that had no cover (0), < 25% cover (1), 25-50% cover (2), 51-75% cover (3) and >75% cover (4). If a nest was found after clutch completion, the date of egg-laying was estimated by floating the eggs in lukewarm water (see Székely et al. 2008). The sea was the only water source and the sea distance was measured using the GPS unit to estimate the perpendicular distance to the nearest part of the coast.

***Recording incubation behaviour***

Both parents were captured on the nest on the same day or on subsequent days using funnel traps, and they were marked with 1-3 colour rings and one metal ring provided by (SWC). Parents were sexed based on their dimorphic plumage, males have strong black eye-stripes and breast-bands whereas females are drab (Fig. 1) (Cramp & Simmons 1983). Incubation behavior of parents was recorded by two methods: either by using a Trovan Flex™ Transponder, LID665 decoder (Dorset identification B.V., Aalten, Netherlands) or by using a small Sony digital video camera (Sony Handycam HC44E, Sony Corporation, Japan). The transponder system consisted of a small chip with unique identification code which was glued on the tail of each parent. The antenna of the transponder decoder was buried approximately 3-5 cm under the nest. The antenna was connected to a data logger. A 12 V car battery was used to provide power for the system. Both the data logger and the battery were buried approximately 2 m from the nest. The system recorded every 20 s whether the male or the female was on the nest for at least 24h (n = 27 nests).

The video camera system was used to record the incubation behaviour at five nests in 2008. The camera was positioned about 1 m from the nest. The camera recorded an

image every 20 s and had a manual night-shot for night images. Power was supplied by a car battery (12 V). The camera was covered by a small piece of cardboard and bits of vegetation, whereas all other parts of the system were buried to minimize the disturbance to the parents. The installation of the transponder and camera systems was carried out early in the morning, or late afternoon to avoid heat stress. The installation took about 15-20 min, and parents returned to the nest in a few minutes after leaving the nest.

Incubation behaviour was only recorded at nests category 0 (exposed nests henceforward), or 3 and 4 (>50% shade, covered nests henceforward). MRA scored the nest shade in the field, and AK and CK scored blindly the nest shades two times based on the nest photos, and then the median was taken for each nest. Repeatability, (following Harper 1994) of scores was highly consistent between three scorers (r=0.939, $F_{31,64}$= 47.837, P<0.001,). In total, 24h incubation data were collected at 32 nests (17 covered nests and 15 exposed nests).

**Fig.1** *A male (left) and female (right) Kentish plover incubating at exposed nests in Farasan Island. The crouched posture and the wet belly-feathers are adaptations to their extremely hot breeding environment.*

Only the transponder nests (n=27 nests) were experimentally manipulated for 24h by completely removing nest cover from covered nests (cover-removed nests, henceforth) or by covering exposed nests with bushes which shaded the entire nest scrape, resembling the highest degree of cover found in un-manipulated nests (cover-added nests, henceforth) (Fig.2). 24h incubation data for 20 nests (11 covered nests and 9

exposed nests) were used in this study because seven transponder nests were predated during the manipulation. Manipulation was carried out early in the morning (five nests), or late afternoon (15 nests). Parents took 81.75± 8.52 min to return to the manipulated nests. Therefore incubating parents were given on average 417± 48.6 min to adjust to the change of their nest cover before incubation recording was started. After 24h, the transponder system was removed and nests were returned to their natural cover-type by returning the original bush to the covered nests and removing bushes from exposed nests.

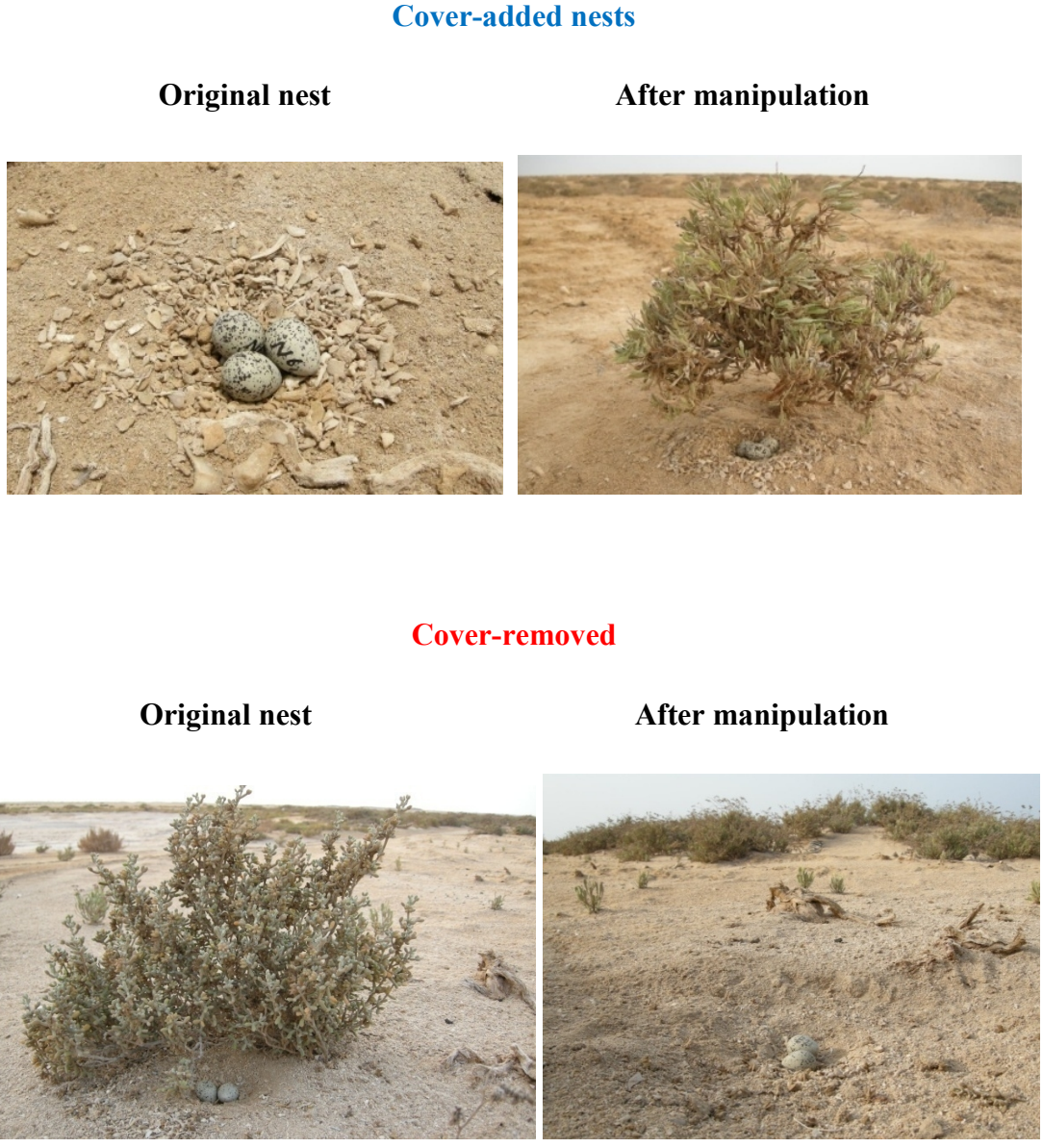


**Fig. 2** *Experimental manipulation of nest cover.*

Ambient ground temperature was measured by a thermo-probe which was placed about 25 cm from each nest scrape at ground level in an open area (n= 32nests). The probe was connected to a data logger (Tinytag, Gemini Data Loggers Ltd.) that recorded the temperature every 20s for at least 24h. Ground temperature often exceeded 50°C at midday (Fig. 3). The maximum ground temperature recorded was 60.3°C.

***Statistical procedures***

Twenty-four hour recordings were considered as the unit of analysis. Each day was divided into 12 two-hour time periods. Four behavioural variables were calculated for each period (see also AlRashidi et al. 2010): (1) total incubation, the percentage of time when the eggs were incubated by either parent; (2) male incubation, the percentage of time when the eggs were incubated by the male, (3) female incubation, the percentage of time when the clutch was incubated by the female, (4) number of changeovers, the number of cases when one parent was relieved by the other parent. The average ground temperature measured outside the nests during each period was taken as the ambient temperature.

First, the influence of natural nest-cover on incubation behaviour (response variable) was investigated using linear mixed-effects models (Pinheiro & Bates 2000). Nest identity was included in the initial models as a random factor, since parental behaviour is not independent between two-hour time periods for a given nest. Nest-cover (factor with two levels: exposed or covered), time period (factor), sea distance (covariate), year (factor), egg laying date (covariate), age of clutch (covariate) and the equipment type (factor with two levels: camera or transponder) were included as fixed effects as they may influence incubation behaviour. Conway & Martin (2000) found that avian incubation behaviour and ambient temperature are not linearly associated, thus ambient temperature was included in the models as second degree orthogonal polynomial covariate. The effect of temperature on incubation may be different over the day (see AlRashidi et al 2010), therefore the interaction between time period and ambient temperature was also included in the initial models. In the initial models of male and female incubation, incubation by the other sex was included as an additional fixed term because in shared incubation systems the behaviour of a parent is influenced by the behaviour of its mate (Kosztolányi et al. 2009).

Percentage variables (converted to proportions) were arcsine square-root transformed, and number of changeovers was ln(x + 1) transformed. The initial models were fitted using maximum likelihood method, and model selection was carried out using the function 'stepAIC' (Venables & Ripley 2002).

Second, the influence of nest cover manipulation on incubation behaviour was investigated using linear mixed-effects models. We used the difference in incubation behaviour after manipulation and before manipulation for the behavioural variables (1-4 as defined above) as response variables. All initial models included nest identity as a random factor, and treatment (with two levels: cover-added and cover-removed) and time period as fixed factors. In the initial models of male and female incubation, the incubation by the other sex was also included as a fixed covariate. Initial models were fitted using maximum likelihood method, and model selection was carried out using the function stepAIC. We used R version 2.10.0 for statistical analyses (R Core team 2010). Values are given as mean ± SE unless stated otherwise.

## Results

### *Incubation behaviour at naturally exposed and covered nests*

Nest attendance (total incubation, male incubation and female incubation) at exposed nests was significantly higher than at covered ones (Fig. 3&4; Table 1&2). In addition, the number of changeovers was higher at exposed nests than at covered ones (Fig. 3; Table 1&2). Age of clutch influenced all incubation behaviours except changeover numbers (Table 1).

### *Incubation behaviour at experimentally manipulated nest cover*

Manipulation of nest cover significantly influenced parental behaviour for all response variables: total incubation, male incubation, female incubation and changeover numbers (Table 3). Parents at cover-added nests reduced incubation efforts whereas parents at cover-removed nests increased incubation efforts compared to the efforts before manipulation (Fig. 5). At cover-removed nests the number of changeovers increased, whereas at cover-added it decreased (Fig. 5).

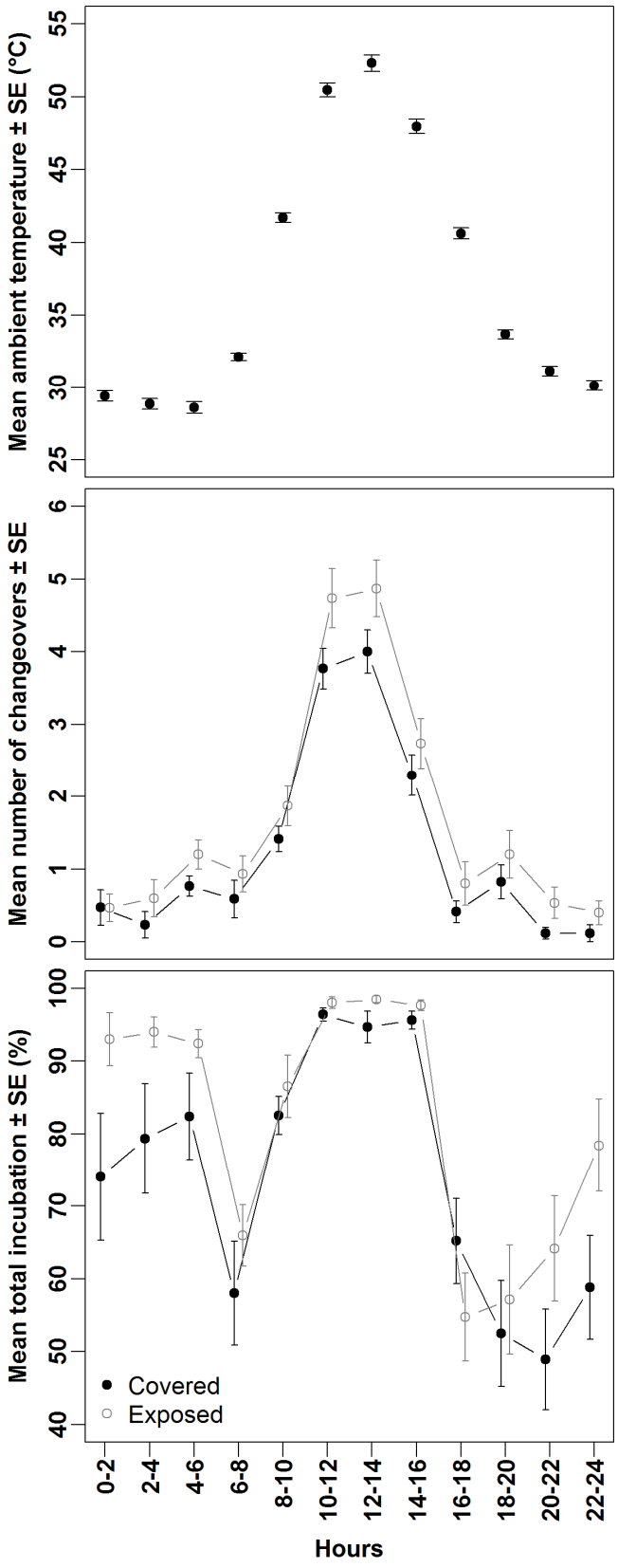


**Fig. 3** *Ambient temperature (top panel), changeover numbers (middle panel) and total incubation (bottom panel) at naturally covered and exposed Kentish plover nests (17 covered nests and 15 exposed nests) in Farasan Island.*

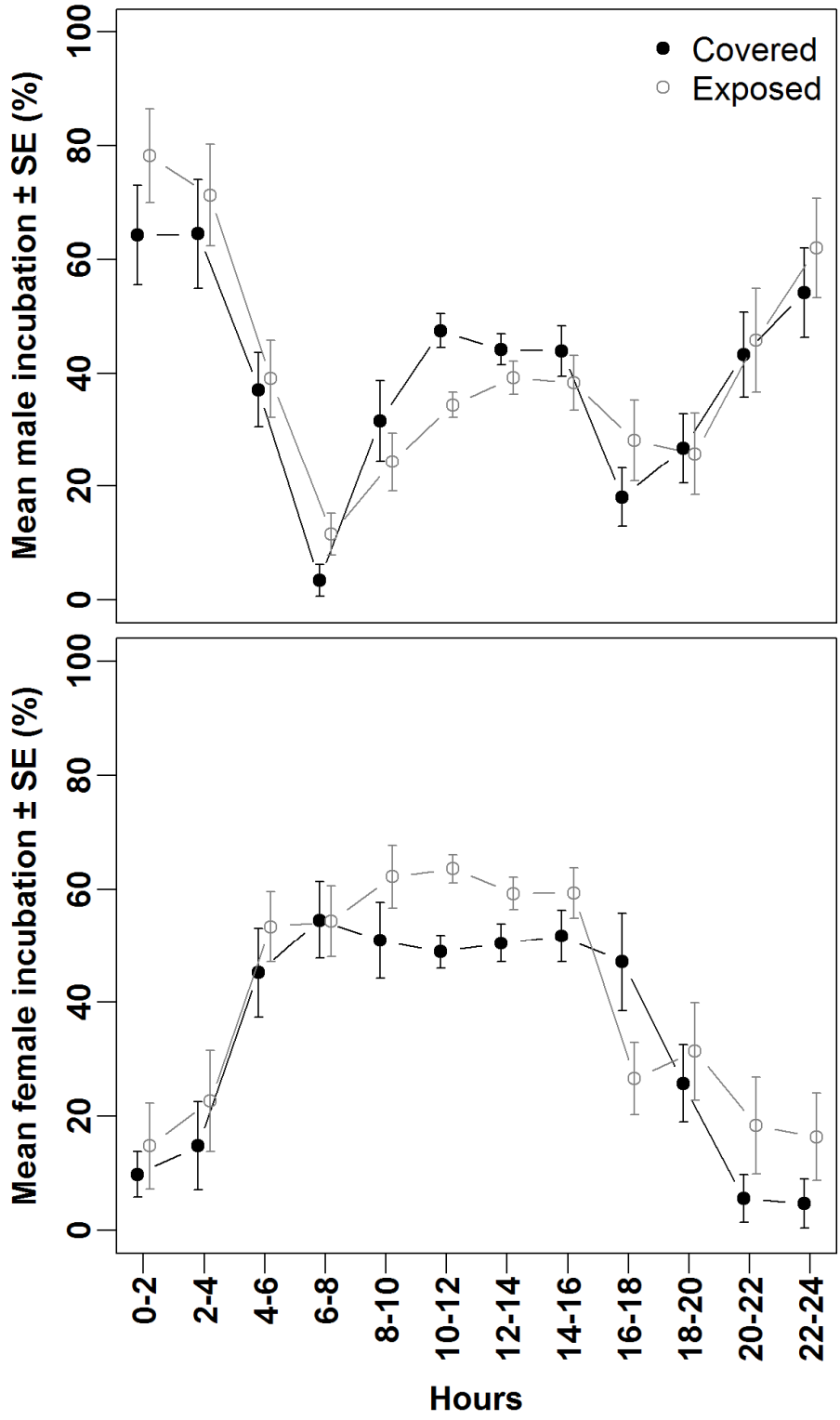


**Fig. 4** *Male (top panel) and female incubation (bottom panel) at naturally covered and exposed Kentish plover nests (17 covered nests and 15 exposed nests) in Farasan Island.*

**Table 1**: *Mean ± SE of four behavioural variables at 32 natural Kentish plover nests (17 covered nests and 15 exposed nests) in Farasan Island.*

| | % total incubation | | % male incubation | | % female incubation | | Changeover numbers | |
|---|---|---|---|---|---|---|---|---|
| | **Mean** | **SE** | **Mean** | **SE** | **Mean** | **SE** | **Mean** | **SE** |
| ***Covered*** | 74.03 | 3.04 | 39.89 | 2.23 | 34.15 | 2.60 | 15.00 | 1.20 |
| ***Exposed*** | 81.69 | 1.96 | 41.50 | 2.56 | 40.20 | 2.40 | 20.33 | 1.77 |

**Table 2**: Results of minimal mixed-effects models for parental cooperation during incubation in 32 natural Kentish plover nests in Farasan Island in 2008 and 2009. (See methods for more details).

| Explanatory variables | Response variable | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | % total incubation | | | % male incubation | | | % female incubation | | | Changeover numbers | | |
| | $df_{error}$ = 339 | | | $df_{error}$ = 316 | | | $df_{error}$ = 338 | | | $df_{error}$ = 317 | | |
| | **df** | **F** | **P** | **df** | **F** | **P** | **df** | **F** | **P** | **df** | **F** | **P** |
| **Cover type** | *1* | *12.21* | *0.002* | *1* | *5.78* | *0.023* | *1* | *11.69* | *0.002* | *1* | *7.60* | *0.010* |
| **Time period** | *11* | *11.22* | *<0.001* | *11* | *1.84* | *0.046* | *11* | *13.86* | *<0.001* | *11* | *2.46* | *0.006* |
| **Ambient temperature** | *2* | *9.07* | *<0.001* | *2* | *6.61* | *0.002* | *2* | *3.67* | *0.027* | | | |
| **Time period x temperature** | | | | *22* | *2.22* | *0.002* | | | | *24* | *2.15* | *0.002* |
| **Female incubation** | | | | *1* | *244.27* | *<0.001* | | | | | | |
| **Male incubation** | | | | | | | *1* | *279.42* | *<0.001* | | | |
| **Age of clutch** | *1* | *17.15* | *<0.001* | *1* | *8.48* | *0.007* | *1* | *15.64* | *<0.001* | | | |
| **Equipment type** | *1* | *7.16* | *0.012* | | | | *1* | *6.82* | *0.014* | | | |

**Table 3:** Results of minimal mixed-effects models for experimentally manipulated Kentish plover nests (cover-added, cover-removed). (See methods for more details).

| Explanatory variables | Response variable | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | % total incubation $df_{error}$ = 220 | | | % male incubation $df_{error}$ 219 | | | % female incubation $df_{error}$ = 219 | | | Changeover numbers $df_{error}$ = 220 | | |
| | **df** | **F** | **P** | **df** | **F** | **P** | **df** | **F** | **P** | **df** | **F** | **P** |
| **Cover manipulation** | *1* | *7.66* | 0.013 | *1* | *4.76* | *0.043* | *1* | *9.39* | *0.007* | *1* | *21.45* | *<0.001* |
| **Female incubation (%)** | | | | *1* | *184.72* | *<0.001* | | | | | | |
| **Male incubation (%)** | | | | | | | *1* | *184.79* | *<0.001* | | | |

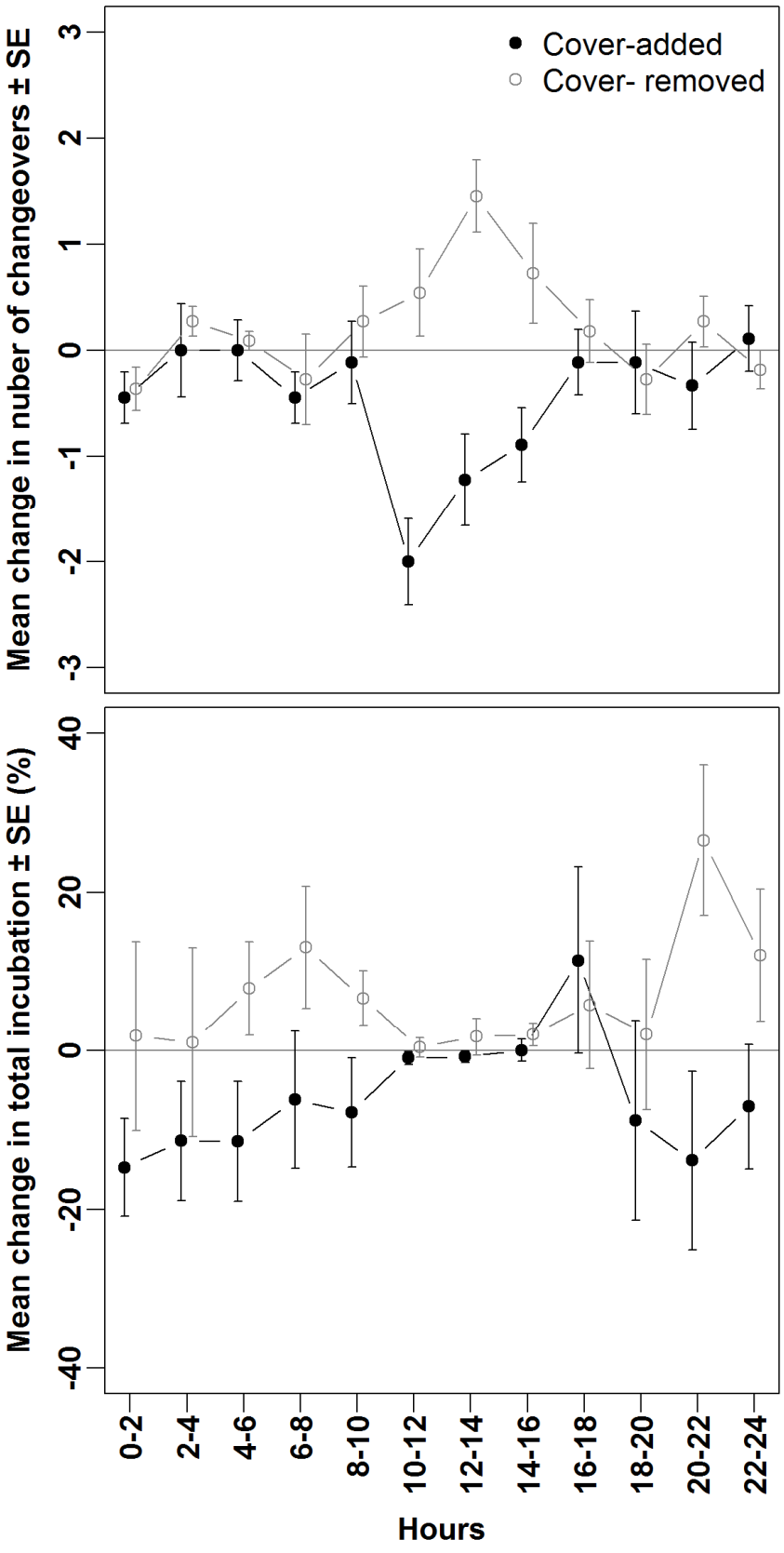


**Fig. 5** *Change in changeover numbers (top panel) and total incubation (bottom panel) ± SE in cover-removed nests (n=11 nests) and cover-added (n=9 nests).*

## Discussion

Our study showed that harsh environment evokes more parental effort and thus facilitate biparental care. Observational and experimental data consistently suggest that nest cover and high temperatures had a significant influence on incubation behaviour. Incubating parents at both exposed and covered nests coordinated incubation behaviour, presumably to prevent their eggs and themselves from overheating (see AlRashidi et al 2010). However, behaviour of parents at exposed nests was more tightly coordinated than at covered nests. The noticeable increase in total incubation and changeover numbers at naturally exposed nests is likely to help the parents avoid heat stress, and to reduce overheating risk both to themselves and to their eggs. By relieving each other frequently from incubation duties parents can do the belly-soaking which plays important roles in thermoregulating the incubating adults and their eggs by cooling the eggs and the parents, and may increase nest humidity (Grant 1982; Amat & Masero 2007; Amat & Masero 2008, Fig. 1).

Interestingly, the diurnal contribution of males to incubation at covered nests was higher than that at exposed nests. This is possibly because males of exposed nests spent more time incubating the clutch at night. We suggest two explanations for the higher nocturnal nest attendance of males at exposed nests. First, an open nest may be safer than a covered nest (Grant 1982; Martin & Roper, 1988; Amat & Masero 2004b), since exposed nests facilitate the detection of predators at night allowing incubating plovers to continue their incubation for long periods. It also facilitates the earlier escaping when predators approach. This is unlikely at our study site. Although, clutch predation was the major cause of Kentish plover breeding failure in our study site 80.10% of nests (n= 196 known fate nests) were eaten by predators, the fate of nests did not differ between covered nests and exposed nests (see Chapter 4). We also did not observe any signs indicate that incubating birds were predated on/near their nests at both two types of nest sites. Second, nest temperature may differ between the two types of nest sites. Bushes may play a role in thermoregulation at night by conserving temperatures to be near egg optimal temperature and thus incubating plovers can leave their nests and invest time for foraging. Temperatures at night were more favourable at covered sites; we found that the average temperatures during night-time (18:00-02:00) inside un-incubated

covered nests was higher (32.30 ± 0.99°C, n=6 periods belong to four nests) than temperatures outside these nests (30.00 ± 0.88, n=6 periods) (Wilcoxon matched-pairs test, $Z = -2.20$, $P = 0.028$). D'Alba and her colleagues (2009) reported that even small changes in the weather conditions at the nest-site can have substantial consequences for reproductive effort. In addition, temperature outside the nest at midnight sometimes fell below 28°C, which is critical for embryo survival in most avian species (Carey, 2002) (Fig. 1), and thus eggs at exposed nests may require warming. Along with that, exposed nests were attended less than covered nests only in evening (16:00-18:00) (Fig.1), this is probably because temperature is within optimal temperature for embryo development for most of bird species which ranges from 36°C to 40.5°C (see Fig.1). Consequently, both parents can leave the nest to forage which was also reported from the closely related snowy plover *Charadrius nivosus* (Purdue 1976).

Our results are not in line with the study of Amat and Masero (2004a) who used the frequencies of captured males on nests during midday in naturally covered and exposed sites to conclude that probability of males' diurnal incubation increased at exposed nests, but not at covered ones. In addition, Amat and Masero (2004a) found that in covered sites plovers did not show any thermoregulatory behaviour whereas we observed some incubating parents of covered nests doing the belly-soaking during the hottest part of the day. Both of these differences may be attributed to the fact that the Farasan Islands are hotter than Fuente de Piedra Lake (southern Spain) where Amat and Masero carried out their study.

Our results are partly consistent with our previous study (AlRashidi et al. 2010) which was carried out in Al Wathba (United Arab Emirates), another extreme hot location where Kentish plovers nest at exposed sites. The results of exposed nests of this study seem to be identical with results of our previous study except in male incubation. In Al Wathba incubation was shared approximately equally between the male and the female during midday but in this study male contributed less. This may be because males of exposed nests in the Farasan Island incubate more at night.

Our results are consistent with the studies that showed that a harsh breeding environment can select for biparental care. Recently, Brown et al. (2010) found that in frogs, biparental care was essential to tadpole survival in small (but not large) breeding pools because small pools contained insufficient nutrients for tadpole growth and

survival. In addition, Wynne-Edwards (1998) found that care by both parents was critical to protect pups and parents alike from hostile weather conditions in a dwarf hamster species *Phodopus campbelli* that breeds in an extremely cold and arid environment (Tuva Autonomous Region, Russia) where ambient temperatures may reach below -30°C.

In conclusion, our results suggest that harsh environments may shape social traits because they require special adaptations which lead to differences in mating systems and types of parental care. Variation in the level of biparental incubation is not constrained by only one environmental factor but it may relate to a combination of several environmental factors. Nest exposure in association with extreme hot temperatures may favour cooperation between incubating Kentish plover parents. Under harsh environmental conditions increased parental cooperation is essential, since a single parent cannot protect the eggs and/or itself from overheating at exposed sites. Experimental analyses of male-female interactions, and comparing the incubation responses of males and females across different plover populations are important avenues for revealing the complex relationships between environmental factors, parental cooperation and sexual conflict.

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# Chapter 4

# Breeding ecology of the Kentish plover *Charadrius alexandrinus* in the Farasan Islands, Saudi Arabia

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**MAR**: data collection, statistical analysis, manuscript writing

**AK**: comments on manuscript

**MS**: comments on manuscript

**TS**: comments on manuscript, general editing

## Abstract

Breeding behaviour and ecology of a small shorebird, the Kentish plover *Charadrius alexandrinus,* were investigated in three consecutive years in the Farasan Islands, Saudi Arabia. In the Farasan Islands Kentish plovers breed either under halophyte bushes or in exposed sites where ground temperatures may reach 60°C. The Kentish plover and its close relative, the snowy plover *Charadrius nivosus*, have been intensely studied in Europe, Asia and America, and these studies provide excellent bases to compare the behaviour and ecology between different populations. The extreme hot environment and the abundance of halophytic bushes offer excellent opportunities to test costs and benefits of nest site choice in this ground-nesting shorebird. Three aspects make the Farasan Island population of Kentish plover distinct from most other populations studied to date. First, incubating plover seem to prefer nesting under halophytic bushes rather than at exposed sites since 177 nests were under bushes, whereas 95 nests were fully exposed sites. Second, both mate fidelity and nest-site fidelity were high, and pairs stayed within short distances from their previous nest sites. Third, brood desertion was very rare in the Farasan Islands – unlike in most other populations where the female or the male deserts the brood – since in 95% of broods both parents attended the chick(s) (n = 153 broods). We argue that these social traits are driven by the extreme hot environment that requires parental cooperation, although adaptation to island-dwelling and corresponding changes in life-history traits can not be ruled out.

## Introduction

The Kentish plover *Charadrius alexandrinus* is a small ground-nesting shorebird that has an extremely large geographic distribution that includes Europe, Asia and Northern Africa (del Hoyo et al. 1996, Wetlands International 2006, Delany et al. 2009). Although Kentish plovers do not approach the threshold for the population decline criterion of the IUCN Red List (BirdLife International 2010), their populations are known to be declining in much of their range. For instance, some European and African populations such as those in Italy, Romania, Hungary, Bulgaria, Sweden Egypt, Mauritania and Guinea-Bissau are declining (Delany et al. 2009), and this species has disappeared as a breeding bird from the British Isles, Norway and in some parts of Spain (Montalvo & Figuerola 2006). Several factors have been identified as contributing to the decline of Kentish plover populations. The major drivers of change are mediated through the transformation, degradation and loss of coastal habitats, disturbance by human activities and predation (Dalakchieva, 2003; Montalvo & Figuerola 2006; Delany et al. 2009; BirdLife International 2010).

Kentish plovers have unusually diverse breeding system among birds (Székely et al. 2006). Both parents incubate the eggs, although after the eggs hatch one parent (usually the female) may deserts the family and seeks a new mate. Therefore, variation in both mating system (monogamy, polygyny and polyandry) and brood care (biparental, male-only and female-only) may all occur within a single population (Lessells 1984; Székely & Cuthill 1999; Kosztolányi & Székely 2002; Székely et al. 2006; Amat et al. 2008). Variation in parental care may be caused genetically (e.g. gene frequencies are different between populations) and/or in response to the environment the plovers inhabits. Recent studies have highlighted that several environmental factors can influence the distribution of care types in Kentish plovers. Biparental care was proposed to be associated with hot ambient temperatures, competition between plover families and high predation risk on chicks (Székely & Cuthill 1999; Székely et al. 1999; Kosztolányi et al. 2006; Amat et al. 2008; AlRashidi et al. 2010). Understanding the causes of this variation in breeding systems both across and within Kentish plover populations is necessary to predict how parental care may respond to environmental changes.

Kentish plovers usually nest in open habitats, although in some populations they also utilise cover so that the nests are under a small shrub (Fraga and Amat 1996; Amat and

Masero 2004a).This diversity in nest sites may be associated with parental condition and/or environment (high ambient temperature and/or predation risk; see Chapter 3). This diversity may lead to variation in parental behaviour and care, egg patterns of development and adult survival (Amat and Masero 2004 a & b). Therefore, a great attention should be paid to investigating variation in parental care both across and within Kentish plover populations in an ecological setting.

The aims of our study were: 1) to collect baseline data on behaviour and breeding ecology of Kentish plover in Farasan Islands, since these data are largely missing. The only published account of this species in Farasan Islands reported that it breeds in the Islands but gave no details (PERSGA/GEF 2003), 2) to investigate the breeding ecology and parental behaviour of this species in an extremely hot environment. We conjectured that the hot environment influences breeding success, distribution of care types, and mate and nest-site fidelity.

## Study area

Fieldwork was carried out between 8$^{th}$ and 19$^{th}$ of July (2007), 17$^{th}$ of April and 4$^{th}$ of July (2008), and 15$^{th}$ of May and 4$^{th}$ of July (2009).We collected data in each year on the largest island of Farasan Islands, Farasan (369 km$^2$) and in 2008 we extended fieldwork to the second largest island, Sagid (109 km$^2$, Fig. 1). These two islands are inhabited with a total population of about 4500 people. The Farasan Islands are an archipelago that is located in the Red Sea about 50 km from the city of Jizan, Saudi Arabia. The archipelago is a protected area established in 1996 by the Saudi Wildlife Commission (SWC), and covers an area of 3,310 km$^2$. It is recognised as an Important Bird Area by BirdLife International (PERSGA/GEF, 2003). Farasan Islands have a subtropical desert climate, with sparse rainfall and average annual precipitation of less than 50 mm, but being surrounded by the sea, are humid all year round (NCWCD, 2000). These islands comprise a variety of habitat types including mangrove, wet and dry salt marshes, sand dunes, sand plains and rocky habitats (El-Demerdash 1996). Vegetation is dominated by halophyte plants such as *Halopeplis perfoliata, Zygophyllum album, Zygophyllum coccineum, Zygophyllum simplex, Limonium axillare, Suaeda monoica*. The degree of grazing pressure by wild Farasan Island gazelles

*Gazella gazella farasani* and domestic herds (e.g. goats and camels) is minor, thus these plant species are abundant, covering a huge area of salt marsh and sand dunes and providing nesting sites for shorebirds (NCWCD 2000).

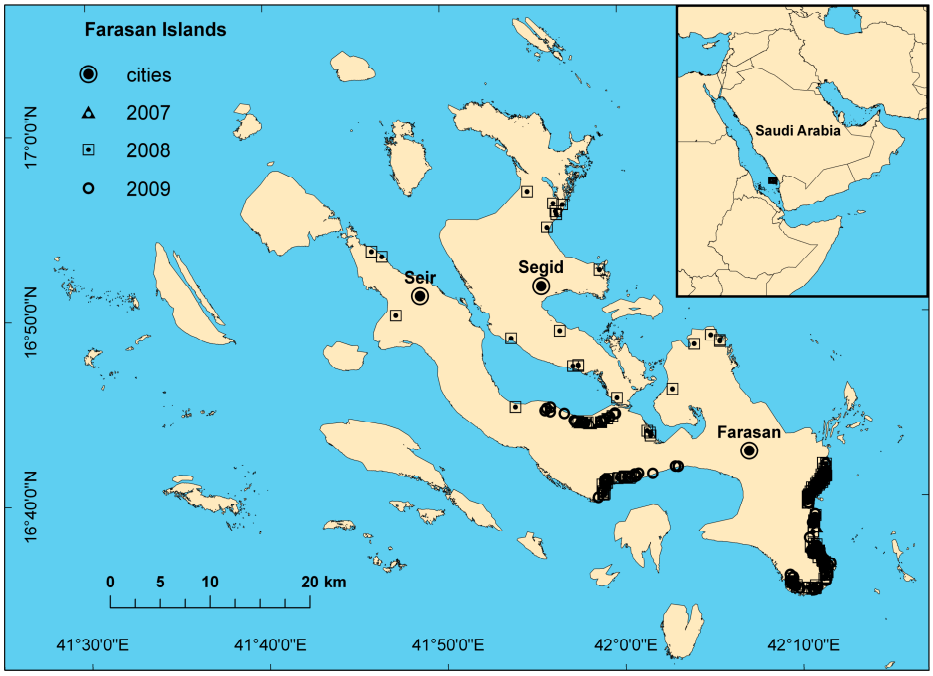


**Fig. 1** *Map of the Farasan Islands showing the locations of Kentish plover nests.*

## Methods

Kentish plovers breed sparsely up to 1 km away from the shore either under bushes or in open areas. Searching for nests was difficult, because the suitable area for the nesting was huge, and there were many bushes which made difficult to spot incubating adults. Two methods were used to locate nests: 1) by driving a car and flushing the incubating birds. Some plovers continue incubating until the car was only few meters from them. Consequently, to avoid damaging the nest, the car was driven slowly, and stopped frequently, and a walk was made about 100 m around the car to spot flushed plovers. 2) By watching incubating birds when they visited the sea to soak their belly, a behaviour that occurs between 10.00 and 15.00 (local time, GMT + 3 hours), and following these parents back to their nests. Once a nest was found, it was photographed and its location was recorded using a hand held GPS unit. Nests were allocated to five cover categories: completely exposed nests that had no cover (0), < 25% cover (1), 26-50% cover (2), 51-

75% cover (3) and > 75% cover (4). Temperature was measured near 32 nests by a thermo-probe which was placed about 25 cm from the nest scrape in an open area at ground level. The probe was connected to a data logger (Tinytag, Gemini Data Loggers Ltd.) that recorded the temperature every 20s for more than 24 hours. The maximum ground temperature recorded was 60.3°C, and ground temperature often exceeded 50°C at midday. Transponder systems and a small Sony digital video camera were used to record incubation behaviour of parents at some nests (see Chapter 3 for more details). The sea was the only water source and the sea distance was measured as the perpendicular distance to the nearest coast. Sea distance was divided to 9 categories 100 m each.

Clutch size and egg sizes were also recorded. Egg flotation was used to estimate the date of egg laying (see Székely et al. 2008). Most nests were visited every 2-5 days. The fate of the clutch was assigned to one of the following categories: (1) Hatched when at least one egg hatched, (2) Predated when the eggs were eaten, (3) Failed when no eggs hatched but the reason of failure was not predation, (4) Abandoned when no adults were observed at the nest, or there were no plover footprints around the nest, or (5) Unknown when the fate of the nest was not followed or the eggs disappeared although neither predation nor hatching was confirmed.

We used Generalized Linear Models (GLMs) with binomial error to test whether nest fate (hatched or predated) differ between nest cover categories. Sea distance, egg laying date and years may all affect nest fate, so we included these variables in the initial models.

Parents were captured by funnel traps on the nest, or with downy chicks (see Székely et al. 2008). The chicks were covered by a sieve large enough to accommodate all young, and the funnel trap was put around the sieve. Adult plovers were ringed with a metal rings provided by (SWC), Saudi Arabia, and 1-3 coloured rings. Chicks were ringed by only two rings, a metal ring and a colour one. Body mass was measured with a Pesola spring balance, the right tarsus length with sliding callipers, and the right wing length (only for adults) with a wing ruler. We did not attempt to follow colour-ringed families, although when a brood was encountered, the sex, the number of attending parents and the number of chicks were recorded. Some chicks also were recaptured and their weight

and right tarsus length were recorded again. Adult males and females were usually straightforward to distinguish. For further methods, see Szekely et al. (2008).

We caught individuals at different stages of incubation to test whether their body mass, right wing length and right tarsus length differed between nest cover categories using multivariate analysis of variance (MANOVA). We created a multivariate response variable (body condition) by binding together the three response variables (body mass, right wing length and right tarsus length). Parents may lose more mass as the incubation period progresses, and so incubation stage was included in the initial model.

Statistical analyses were carried out using R 2.10.0 (R Development Core Team 2010) and SPSS 17.0. For non-parametric data we provide the median (M), the lower quartiles (LQ) and the upper quartiles (UQ).

## Results

### *Clutches and nest fate*

In total 272 nests were found: six nests in 2007, 162 nests in 2008 and 104 nests in 2009. Most eggs were laid in May and June. Some chicks were captured at the beginning of the fieldwork in 2008. Therefore, based on the estimated ages of chicks and egg-lying date, the breeding season may start as early as February, and it may last until late August. Kentish plovers breed in areas with no or little mangrove *Avicina marina*, and most nests (n=162 nests) were found in the eastern part of the main island where there were no mangrove trees (Fig. 1). 177 nests were under halophytic bushes, whereas 95 nests were fully exposed sites. Bushes may serve as a shelter from the direct solar radiation, since about 35.7% of nests had very good to excellent shade (categories 3-4), and they may also make nests cryptic for predators. 9.9% of them had a little shade covering less than 25 % (category 1, Fig. 2). Nest distance from the sea ranged from 5 m to 850 m. The number of nests decreased exponentially with the distance from the sea (Exponential regression: $r^2 = 0.98$, $F_{1,7} = 303.28$, $P \leq 0.001$, n = 272 nests, Fig. 3).

Out of 190 completed nests 100 had three eggs, 79 had two eggs and 11 had only one egg. Clutch sizes did not differ between the nest cover categories (Kruskal–Wallis test, $\chi^2 = 2.23$, df = 4, $P = 0.693$).

The fate was known for 196 nests (Table 1). Predation was high since 80.1% of the nests were eaten by predators (n=157 nests) whereas only 14.8% of clutches produced chicks (n=29 nests). Nest fate decreased as the breeding season progressed (Fig. 4; GLM with binomial error, B = -0.03 ± 0.01, $P = 0.007$). Nest-cover, years, sea distance and the interaction between nest-cover and sea distance did not influence nest fate ($P > 0.05$) and none was included in the final model.

The majority of the nests (n= 105 nests) were predated by terrestrial predators (stray domestic cats or white-tailed mongooses *Ichneumia albicauda*, their footprints were found around predated nests. Domestic cats were observed near some nests, and nest cameras identified a mongoose (Fig. 5). Three nests were predated by a large bird possibly Indian House Crow *Corvus splendens*, their footprints were found around predated nests. At many nests, however, the predators did not leave footprints so that their identification is unknown. Hoopoe lark *Alaemon alaudipes* destroyed five nests by opening the eggs and throwing them out of the nests. The hoopoe larks attack the eggs when the parents were absent (early morning and late afternoon, Fig. 5). It is unlikely that the presence of the camera and other equipment around the nest attracted the predators, because predation rate of nests with the equipment (70.0%) was lower than that of non-recorded nests ($\chi^2$ test of homogeneity, $\chi^2 = 6.263$, df = 1, $P = 0.012$).

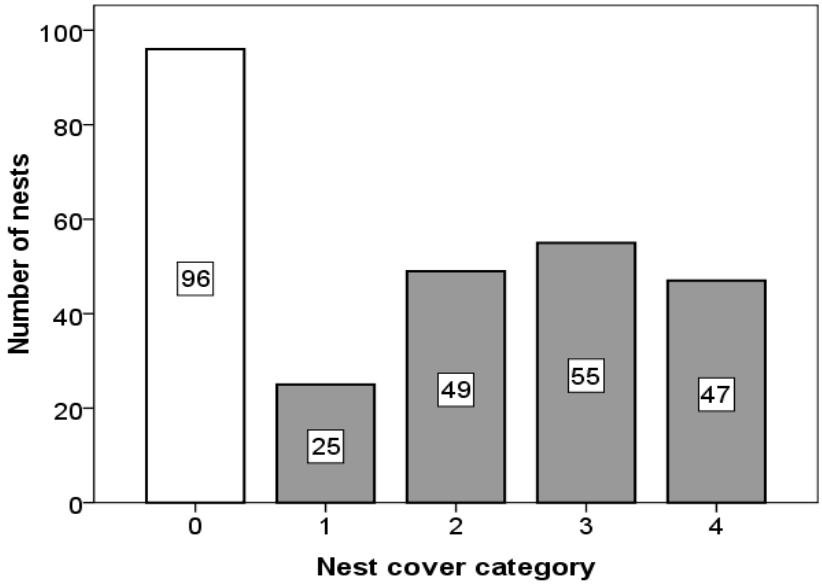


**Fig. 2** *Histogram for 272 Kentish plover nests were found in Farasan islands 2007, 2008 and 2009. Each bar presents the cumulated frequencies of nest numbers for a given nest cover category.*

**Table 1.** *The fate of Kentish plover nests in the Farasan Islands.*

| Year | **Hatched** | **Predated** | **Failed** | **Abandoned** | **Trampled** | **Unknown** | **Total** |
|---|---|---|---|---|---|---|---|
| 2007 | 3 | 1 | | | | 2 | 6 |
| 2008 | 15 | 94 | 2 | 2 | | 49 | 162 |
| 2009 | 14 | 63 | | 1 | 1 | 25 | 104 |

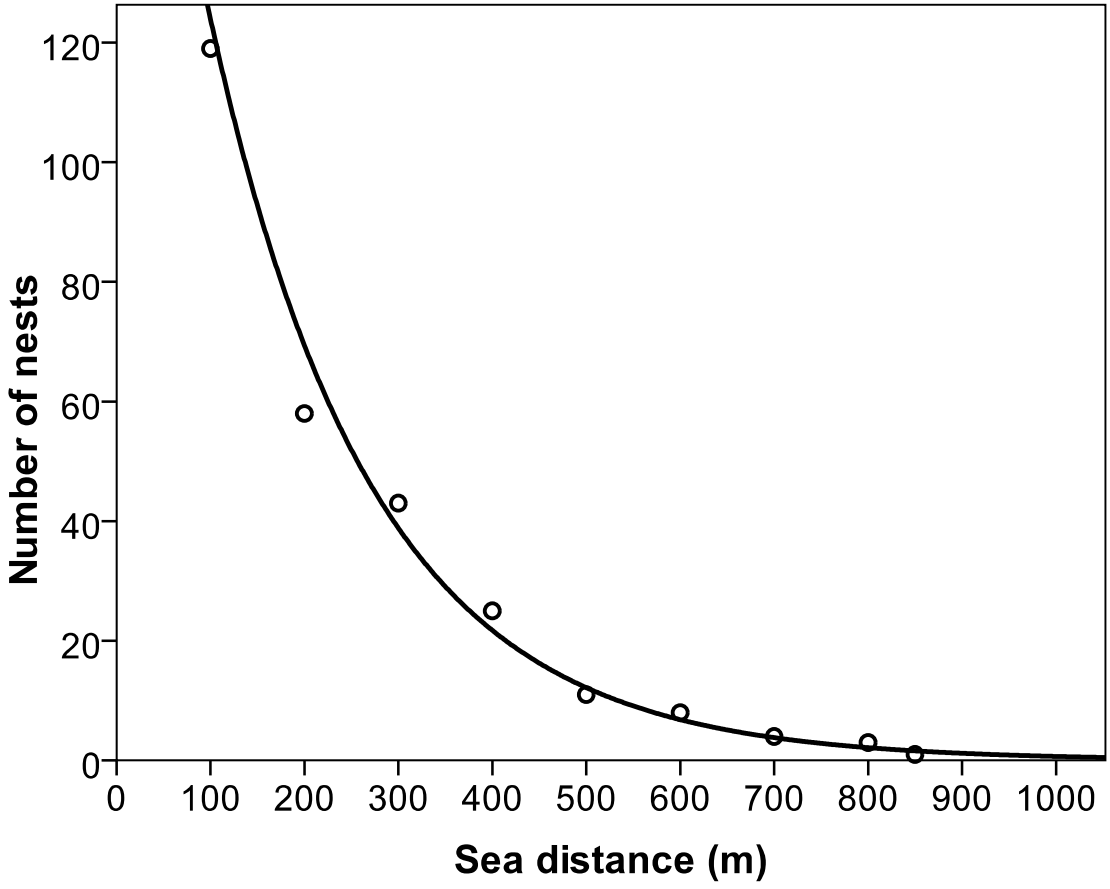


**Fig. 3** *The number of nests in relation to sea distance. Nest numbers decreased exponentially as sea distance increases (see text for details).*

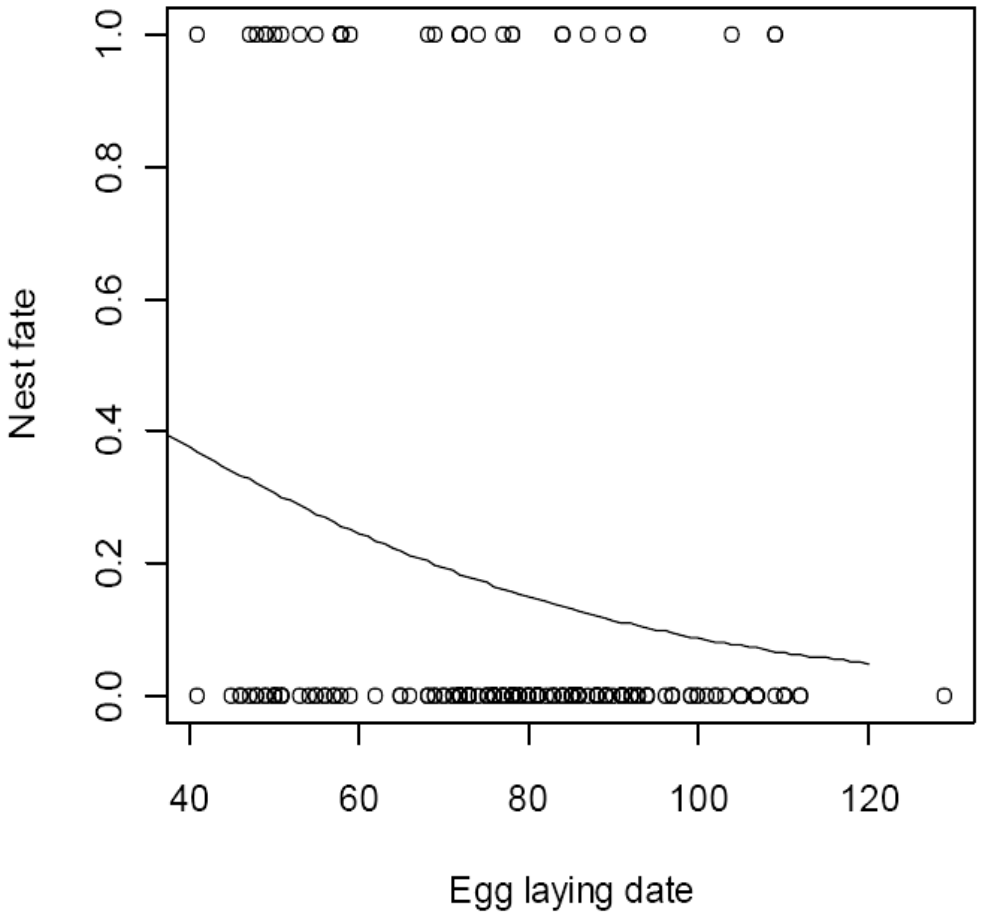


**Fig. 4.** *Fate of Kentish plover nests in relation to egg-laying date in Farasan Islands (1: hatched, 0: predated). The line indicates predicted values of a generalized linear model with binomial error (see text for details). Egg-laying date is given as number of days since 1 March.*

**Fig. 5.** *Egg-shell remains at predated nests by a mongoose (left and middle) and by a hoopoe lark (right).*

***Body condition***

Body condition of males and females (body mass, right wing length and right tarsus length) did not differ between nest cover categories (MANOVAs, males: $F_{3,44}$ =0.41, $P$ = 0.748; females: $F_{3,50}$ =1.65, $P$ = 0.190).

***Brood-rearing***

Kentish plovers have biparental brood care in the Farasan Islands. We trapped 514 Kentish plovers (239 adults and 275 chicks) in 153 families (22 families in 2007, 53 families in 2008 and 78 families in 2009). In all families, both parents were observed or captured with their chicks except in eight families where either the female or the male was absent (n = 5 and 3 families, respectively). We spent between 30-60 min with each family and the absent parent could be with the rest of chicks or incubating un-hatched eggs. If only one chick was captured, one parent stayed around the trap whereas the other leaded the other chicks away. In some nests that were far away from the sea, when one eggs hatched, one parent took the chick to the sea whereas the other parent continued incubating the eggs. The chick age of all families ranged from one day at hatching to about 40 days when chicks can fly. In three families which were re-sighted until the chicks became 40 days old, both parents stayed with their chicks. In another ten families the chicks were recaptured within 10-20 days from the first capture and both parents were sighted with their chicks.

***Mate fidelity and site fidelity***

Kentish plovers kept their mate for several breeding attempts. Both parents were ringed in 63 pairs in 2008, in 24 pairs out of which both parent were recaptured in 2009. In 19 pairs out of 24, the pair stayed together whereas in 5 pairs they divorced. Two pairs of the 19 pairs re-nested in the same nest scrape, these two pairs were out of only 15 pairs that nested successfully in 2008, whereas the other pairs moved to new sites 105 (median) (70 -157.5 m, (LQ–UQ), n = 17 pairs). Five pairs of which nested in covered sites re-nested with almost the same cover type whereas four pairs moved from exposed sites to covered ones. Two of these four pairs were experienced nests failure in 2008

and one nest was manipulated by covering it with an excellent cover in 2008, this may lead them to change their nest covers (Spearman rank correlation coefficient between 2008 nest-cover and 2009 nest-cover, rs = 0.124, N = 9, P = 0.751).

Three males and two females that changed their mate between 2008 and 2009 moved to new sites; one female moved 600m from its previous nest scrape, and the other 155m whereas the males moved (145 (65 -160 m), n = 3 males).

In 2008, three pairs that lost clutches in the beginning of breeding season re-nested together late in the season in another scrape with the same nest cover type.

In 2009 one of 11 pairs that were ringed in 2007 re-mated with the same partner, and their nest was 215 from their previous nest; although we have no information about this pair from 2008.

## Discussion

Our study provided several important results. Firstly, clutch predation was very high. Nest failure was primarily attributed to mammalian predators, mainly white-tailed mongoose and stray cats. In the Farasan Islands, white-tailed mongoose causes nest failure not only for Kentish plover but also for the other ground-nesting birds including osprey *Pandion haliaetus* (NCWCD 2000; PERSGA/GEF 2003). We argue that although mongoose may be a natural mammalian predator in Farasan Islands, it may achieve unnaturally high densities due to availability of food, particularly domestic garbage. We suggest that to improve nest success of birds, the number of mongooses should be controlled. Alternatively, some islands should be made predator free by eradicating mongooses and cats.

Secondly, parents seem to prefer nesting under bushes rather than at exposed sites. This behaviour appears to be different from the Kentish plovers in Spain as reported by Amat and Masero (2004a). Despite the abundance of *Arthrocnemum* at Fuente de Piedra, the main plant used for nest cover, they found most of Kentish plover nests in sites with little or no cover. We suggest two explanations for this difference. First, midday temperatures may be higher in the Farasan Islands than in Fuente de Piedra which may select for nesting under bushes (see Chapter 3). Second, many shorebirds nest in

exposed or semi-exposed sites to minimize predation risk, on both nest contents and incubating adults alike because such these sites facilitate early detection of predators (Grant 1982; Burger 1987; Ward 1990; Amat and Masero 2004a). Although clutch predation was almost similar and nest fate did not differ between covered nests and exposed ones neither at Fuente de Piedra Lake nor in Farasan Islands, predation on incubating plovers at Fuente de Piedra Lake appears to be higher than it in Farasan Islands. Amat and Masero (2004a) reported that some adults were predated on/near their nests and most of which were at covered sites whereas we did not observe any signs indicate that incubating plovers were predated on/near their nests. Since eggs at covered nests and exposed ones predated at a similar rate in Farasan Islands and there was no risk on incubating plovers in both types of nests, Kentish plover breeders which experienced clutch predation at exposed sites may move to nest under bushes because there was no advantage of nesting at exposed sites (see results, nest site fidelity).

Thirdly, in some bird species, parents in poor body condition may accept nesting in less preferred nest-sites (Wiebe & Martin 1998; Amat & Masero 2004a; D'Alba et al. 2009). Amat and Masero (2004a) found that Kentish plover females that nested in covered sites were in lower body condition than those nesting in exposed sites, and they argued that those females were unable to withstand the high ambient temperatures in exposed sites. Our results show breeders did not show any significant differences in body mass, the wing length and the tarsus length between exposed and covered nests.

Fourthly, brood desertion in Farasan Islands is rare and thus biparental care was more common in this population than in temperate zone populations (Lessells 1984, Székely & Lessells 1993). Moreover, both parents appear to stay with their chicks longer than those on the other populations (Fraga & Amat 1996; Kosztolányi et al. 2009).We suggest three explanations why brood desertion is rare in this population. First, mate availability may be low in the Farasan Islands and thus the deserting parent may have no chance of remating and raising another brood. Given that mate availability is depend on adult sex ratio and brood care patterns (McNamara et al. 2002), it is important to estimate the adult sex ratio in the future. Second, hot temperatures especially at midday may favour shared brood care, both parents are needed to brood and shade the chicks to avoid overheating (Kosztolányi et al. 2009). However, this may not be a likely explanation in the Farasan Islands, because chicks may cool themselves by bathing in the sea or moving under the abundant bushes. Third, competition between plover

families, food distribution and high predation on the chicks may favour biparental care with high parental cooperation (Fraga & Amat 1996; Kosztolányi et al. 2006; Kosztolányi et al. 2007). We observed fights between neighbouring families and some chicks were injured. This occurs usually when the tide raises, and the foraging area shrinks and thus the plovers and other shorebirds concentrate in a small strip of shoreline. Infanticide by adults has been reported in several populations (Fraga & Amat 1996; Székely & Cuthill 1999). Kosztolányi et al. (2006) found that when food distribution was patchy, the density of plovers and competition between plover families increased, parents spent more time defending their chicks. In addition, Fraga and Amat (1996) found that biparental care lasted for about 20 days at Fuente de Piedra because of heavy predation on chicks by gull-billed terns *Sterna nilotica,* and they argued that both parents may protect their young better than a single one by chasing gull-billed terns away from the brood and by distracting the predator's attention.

Finally, although nest predation was high and the breeding season was almost continuous and lasted for long period (up to 7 months), we found high mate fidelity and nest-site fidelity. Breeding failure may induce low nest-site and mate fidelity (Warriner et al.1986; Haig & Oring 1988; Thibault 1994; Flynn et al. 1999). Length of the breeding season and operational sex-ratio may also influence both nest-site and mate fidelity (Llambías et al. 2008; Lloyd 2008). Our result is partially consistent with the study of Kosztolányi et al (2009) who found high nest-site fidelity but low mate fidelity in Abu Dhabi, where nest predation was high. A possible explanation for the difference between these studies in mate fidelity may relate to a difference in the mate availability between the two populations. Kosztolányi et al (2009) found two cases of divorce between nest attempts within a season whereas we did not observed any cases.

## Conclusions

The Farasan Islands provide some of the most important breeding sites of Kentish plovers in Saudi Arabia. The breeding biology of the Kentish plover appears to be different from other populations. We hypothesise that these differences are largely due to high ambient temperature although we can not exclude alternative explanations. Farasan Island conservation authorities need to control the numbers of domestic cats

and mongooses. This urgent management issue needs quick resolution; we strongly advise to fence some areas on the two largest islands to protect the Kentish plover from these predators. These areas should be large enough (at least 1 $km^2$) to provide safe and adequate nesting sites and brood-rearing sites.

The Kentish plover population in Farasan Islands offers an excellent opportunity to investigate the life-histories of these individuals and it is ideal for long-term monitoring and carrying out specific ecological research. Future research studies should focus on the following topics: (1) investigate the movements and site fidelity of Kentish plovers over a longer time-scale to verify our present findings. (2) Estimate the survival of adults and juvenile Kentish plovers and model population sex ratio. (3) Collect more data on brood care in order to compare the behaviour of Farasan Island Kentish plovers to those on mainland Saudi Arabia. (4) Carry out a long-term study for nest-cover preference of individual parents and their chicks.

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# Chapter 5

# Use of remote sensing to identify suitable habitat for the Kentish plover and estimate population size along the western coast of Saudi Arabia

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*Authors' contributions*

**MAR**: study design, data collection, statistical analysis, manuscript writing

**PRL**: spatial analysis, comments on manuscript

**MO**: comments on manuscript

**MS**: comments on manuscript

**TS**: comments on manuscript, general editing

## Abstract

The identification of the environmental parameters affecting species' habitat preferences is a key to understanding the relationships between habitat features and species' distributions. This understanding can be used to develop guidelines for managing their populations and to underpin future conservation strategies. We used distribution modelling to estimate the population size of the poorly known species in the western coast of Saudi Arabia, the Kentish plover *Charadrius alexandrinus*. We used a Generalised Linear Model (GLM) with four habitat variables derived from satellite data: elevation, distance to settlements, vegetation cover and soil moisture to produce a habitat suitability model. Validation of this model using a receiver operating characteristic plot suggests that it is at least 80% accurate in predicting suitable sites. We then used our estimate of total area of suitable habitat above a critical suitability threshold and data on the Kentish plover density, to estimate the total population size to be 9955±1388 individuals. Finally, we believe that our modelling approach can provide a foundation for conservation planning and long-term population monitoring of Kentish plover and the other shorebirds in this region. We also believe that conservation of Kentish plover habitat will not only protect this species but will benefit other shorebird species in the region, many of which have similar habitat requirements. We recommend that certain highly suitable areas are designated as protected areas.

## Introduction

Shorebirds (sandpipers, plovers, gulls and allies; about 350 species) are distributed globally and can be found on all continents. Shorebirds, by virtue of their life history, behaviour, migratory and foraging habits are important indicators of the integrity of coastal ecosystems (Furness and Greenwood 1993, Piersma and Lindström 2004, Székely *et al*. 2004, Thomas and Székely 2005, Thomas *et al*. 2006). Many shorebird populations are declining, and more than half of all shorebird species are declining globally (International Wader Study Group 2003, Stroud *et al*. 2006). The principle reason for these declines is habitat loss and degradation, but other impacts include climate change, pollution, human disturbance and predation. Recreational beach activities in shorebird habitats cause significant direct and indirect disturbance to nesting birds in many areas (Barter 2002, Delany and Scott 2006, Piersma and Lindström 2004, Stroud *et al*. 2006). There is also the potential for future changes in sea level due to global warming to impact shorelines and the feeding and breeding habitats for shorebirds (Galbraith et al. 2005).

The Kentish plover *Charadrius alexandrinus* is a small ground-nesting shorebird and has an extremely large geographic distribution range that includes three continents: Europe, Africa and Asia (del Hoyo *et al*. 1996; Wetlands International 2006). Although Kentish plovers do not approach the threshold for the population decline criterion of the IUCN Red List (BirdLife International 2010a), their populations are known to be declining in much of their range. For instance, some European and African populations are declining such as those in Italy, Romania, Hungary, Bulgaria, Sweden Egypt, Mauritania and Guinea-Bissau (Delany *et al*. 2009), and this species has disappeared as a breeding bird from the British Isles, Norway and in some parts of Spain (Montalvo & Figuerola 2006). Several factors have been identified as contributing to the decline of Kentish plover populations. The major drivers of change are mediated through the transformation, degradation and loss of coastal habitats, disturbance by human activities and predation (BirdLife International 2010a, Dalakchieva 2003, Delany *et al*. 2009, Montalvo & Figuerola 2006).

The ecology, distribution and temporal trends of the population of Kentish plovers on the western coast of Saudi Arabia are poorly known. No systematic surveys have been conducted to estimate population size, with the only counts available were made in the

winter of 1990. This reported 335- 546 birds near Jizan (BirdLife International 2010b) and 351-500 birds in Farasan Islands (BirdLife International 2010c). Little detailed mapping work has been conducted for the species, although Jennings (1995) provided and 'interim' atlas of breeding sites for along the west coast of Saudi Arabia. The most recent record of this species on this region of Saudi Arabia reported that it breeds in the Farasan Islands but gave no assessment of numbers (PERSGA/GEF 2003).

### *Aims of study*

There were three major aims to this project. First, to use a species distribution model to characterise the relationship between Kentish plovers and the environment and map suitable habitat. Species distribution models over large geographical extents using spatial data derived from remote sensing are important tools in landscape ecology, conservation biology, wildlife management and conservation planning ( Araújo and Guisan 2006, Elith *et al*. 2006, Guisan & Zimmermann 2000, López - López *et al*. 2007, Marmion *et al*. 2008, Zarri *et al*. 2008). Moreover, identification of the environmental parameters influencing species' habitat preferences is useful to understand the relationship between habitat features and species distribution. This can be used to prepare guidelines for managing their populations and develop future conservation strategies (Gibson et al. 2004, Gottschalk et al. 2005, Guisan & Zimmermann 2000).

The second aim was to estimate the density of this species at the suitable sites and to estimate population size on the basis of the predicted area of suitable habitat. Lastly, the research aimed to provide guidance for the development of conservation strategies in the region, and advice for future surveys and monitoring actions.

## Methods

### *Study area*

This research project was carried out on the western coast of Saudi Arabia including the Farasan Islands (Fig. 1). Saudi Arabia's Red Sea coastline extends about 1,840 km from the Jordanian border (29° 30'N) to the border with Yemen (16°22'N) (PERSGA/GEF 2003). The Farasan Islands are an archipelago located in the Red Sea about 50km from

the city of Jizan, Saudi Arabia. It is a protected area established in 1996 by the Saudi Wildlife Commission (SWC) and covers an area of 3,310 km$^2$; it is categorized as an important bird area by BirdLife International (PERSGA/GEF 2003). The study area comprised a variety of habitat types including mangroves, wet and dry salt marshes, sand dunes, sand plains and rocky habitats. The Red Sea coast is arid with extremely high temperatures in the summer. Rainfall is sparse and the average annual precipitation is less than 70 mm (PERSGA/GEF 2003). The Red Sea is a semi-enclosed body of water and has almost no daily difference in tidal height in the centre, but the northern and southern ends show daily differences in spring tide ranges from about 0.6m in the north and up to 0.9m in the south (Sheppard *et al*. 1992).

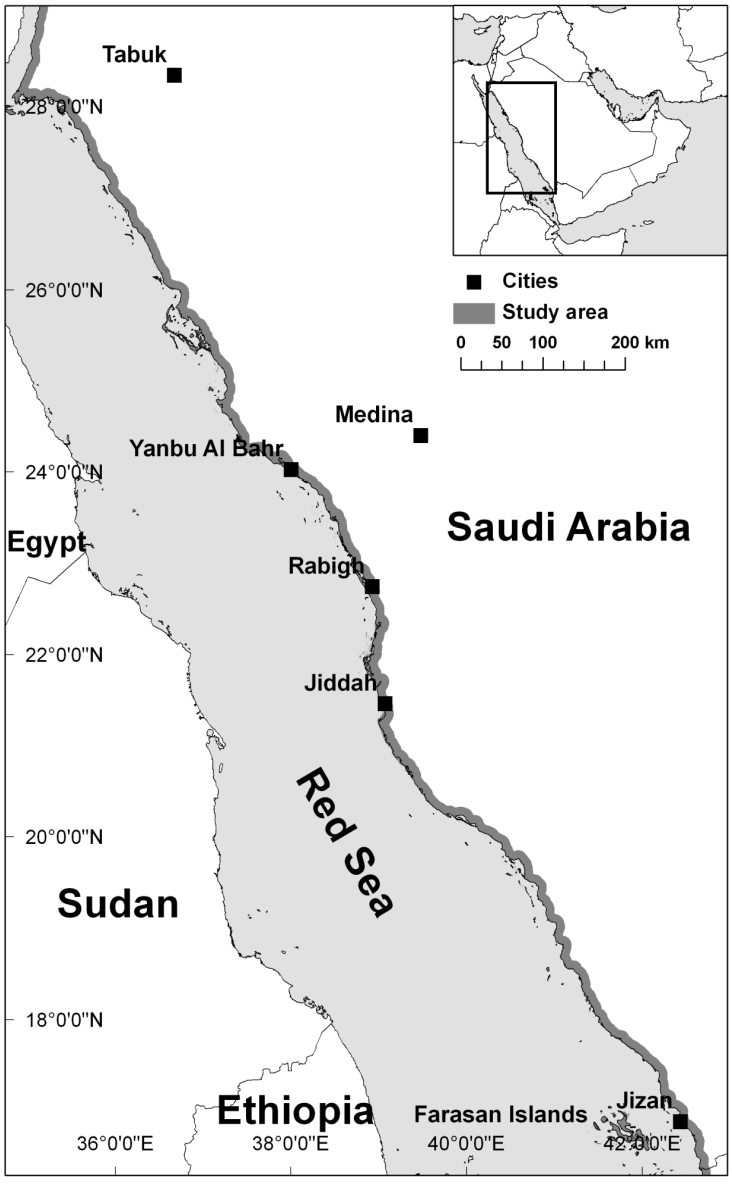


**Fig. 1.** *Location map. The shaded area represents the study area.*

***Fieldwork and data collection***

A coastal survey was conducted between 2 July and 10 August, 2008. The Kentish plover breeding season on the west coast of Saudi Arabia seems to begin in early February and continue until August (see chapter 4). Therefore, we selected this time because it lies toward the end of breeding season of the Kentish plover and it is easy to observe both adults and chicks.

The locations of the start points of sample routes within the study area were stratified randomly with respect to soil moistness derived from satellite data. From each starting point a 2 km sample route was made by driving a four-wheel car at a speed of 10-30 km/h north along the coast from the starting point on the high tide line of beach or as close to it as possible. We used a 2 km route length because it could be surveyed quickly, permitting 98 routes to be surveyed in total. Each transect was repeated twice in the same day. The surveys took place form early morning till late evening (1 h following sunrise to 1 h preceding sunset). We did not take into consideration the tidal cycles because the Kentish plover is not a tide following feeder (Granadeiro *et al*. 2004).

When any Kentish plover (adults or chick) was encountered, within a distance of 250m from either side of the car, the location where each plover was sighted was recorded with a GPS receiver (Garmin e-Trex), the distance to the plover was estimated and the angle was measured clockwise from North to the plover. The track for each line transect was recorded as well.

All sample routes (tracks) were plotted in a GIS, in the UTM 37N reference system using the WGS 1984 datum. Each track shapefile was converted to a raster grid within the GIS. A 500 m buffer was then created around each track to describe the environment in immediate vicinity of the birds, generating a set of cells that are used by Kentish plovers. These were then converted to a Boolean raster in which the presence cells were coded as 1 and all other cells received a value of 0.

**Table 1.** Landsat scenes used in this study

| Path/row | Date | Sensor | Satellite | ID |
|---|---|---|---|---|
| p167r47 | 21-Jun-2000 | ETM+ | Landsat7 | L7CPF20000401_20000630_08 |
| p167r48 | 05-Apr-2001 | ETM+ | Landsat7 | L7CPF20010401_20010630_05 |
| p167r49 | 09-Sep-2000 | ETM+ | Landsat7 | L7CPF20000719_20000930_09 |
| p168r46 | 27-May-2000 | ETM+ | Landsat7 | L7CPF20000401_20000630_08 |
| p168r47 | 28-Apr-2001 | ETM+ | Landsat7 | L7CPF20010401_20010630_05 |
| p168r48 | 13-Aug-1999 | ETM+ | Landsat7 | L7CPF19990701_19990930_14 |
| p169r45 | 23-Sep-2000 | ETM+ | Landsat7 | L7CPF20000719_20000930_09 |
| p169r46 | 03-Jun-2000 | ETM+ | Landsat7 | L7CPF20000401_20000630_08 |
| p170r43 | 14-Sep-2000 | ETM+ | Landsat7 | L7CPF20000719_20000930_09 |
| p170r44 | 12-Jul-2000 | ETM+ | Landsat7 | L7CPF20000701_20000718_08 |
| p170r45 | 01-Nov-2000 | ETM+ | Landsat7 | L7CPF20001001_20001231_07 |
| p171r42 | 23-Oct-2000 | ETM+ | Landsat7 | L7CPF20001001_20001231_07 |
| p171r43 | 23-Oct-2000 | ETM+ | Landsat7 | L7CPF20001001_20001231_07 |
| p171r44 | 23-Oct-2000 | ETM+ | Landsat7 | L7CPF20001001_20001231_07 |
| p172r41 | 12-Sep-2000 | ETM+ | Landsat7 | L7CPF20000719_20000930_09 |
| p172r42 | 10-Jul-2000 | ETM+ | Landsat7 | L7CPF20000701_20000718_08 |
| p172r43 | 10-Jul-2000 | ETM+ | Landsat7 | L7CPF20000701_20000718_08 |
| p173r40 | 01-May-2001 | ETM+ | Landsat7 | L7CPF20010401_20010630_05 |
| p173r41 | 05-Oct-2000 | ETM+ | Landsat7 | L7CPF20001001_20001231_07 |
| p174r40 | 10-Sep-2000 | ETM+ | Landsat7 | L7CPF20000719_20000930_09 |
| p174r41 | 10-Sep-2000 | ETM+ | Landsat7 | L7CPF20000719_20000930_09 |

***Environmental variables***

Remotely sensed digital datasets provide a useful tool for identifying areas of suitable habitat. In particular, vegetation cover, topography and human structures can be quantified to measure the size, extent and spatial pattern of habitat features, and predict a species' realized ecological niche (Guisan & Zimmermann 2000; López-López *et al*. 2007).

We selected four habitat variables to be used in the model; elevation, distance to settlements, vegetation cover and the soil moisture. We used Landsat 7 data because they have an appropriate spatial and spectral resolution, and are readily available for the study area. In order to cover the entire study area, we used 21 Landsat 7 scenes acquired in summer 1999, 2000 and 2001 (Table 1). It was not possible to find a set of images collected in the same year which were free of cloud cover because of the large study area. The source for this dataset was the Global Landcover Facility (http://www.landcover.org). Bands 1, 2, 3, 4, 5 and 7 were mosaiced separately and then clipped to within the west coast of Saudi Arabia, The total study area was 1078 $km^2$ (Fig. 2). All image processing work used Idrisi Kilimanjaro (Eastman 2003).

The tasseled cap transformation (Kauth & Thomas 1976) is a useful tool for reducing the number of dimensions of satellite data and extracting biologically meaningful environmental indices (Crist & Cicone 1984). We used a tasseled cap transformation using coefficients for the Landsat ETM+ sensor (Huang *et al*. 1998) to produce two rasters: tasselled cap greenness showing the amount of green vegetation and tasselled cap moistness which describes the amount of soil moisture (Fig. 2). Finally, all transformed images were rescaled such that pixels took digital number values from 0 to 255.

Elevation data were derived from the Shuttle Radar Topography Mission (SRTM). Tiles of SRTM data corresponding to the 21 WRS-2 scenes of Landsat data used were downloaded from the Global Landcover Facility (http://www.landcover.org). These were then mosaiced and clipped in the same way as the satellite images. The resolution of this dataset was 90 m, but in order to overlay all layers of environmental data exactly, we resampled the SRTM to 30m resolution to produce the final elevation map (Fig. 2).

As a proxy measure of human impact, we made a data layer showing distance to the nearest settlement. A point shapefile containing all settlements in western coast of Saudi Arabia was projected to UTM 37N and clipped to the study area. The source of these data was http://www.gospatial.com. We then converted the data to raster format in which each cell took as its value the distance (km) to the nearest settlement (Fig. 2).

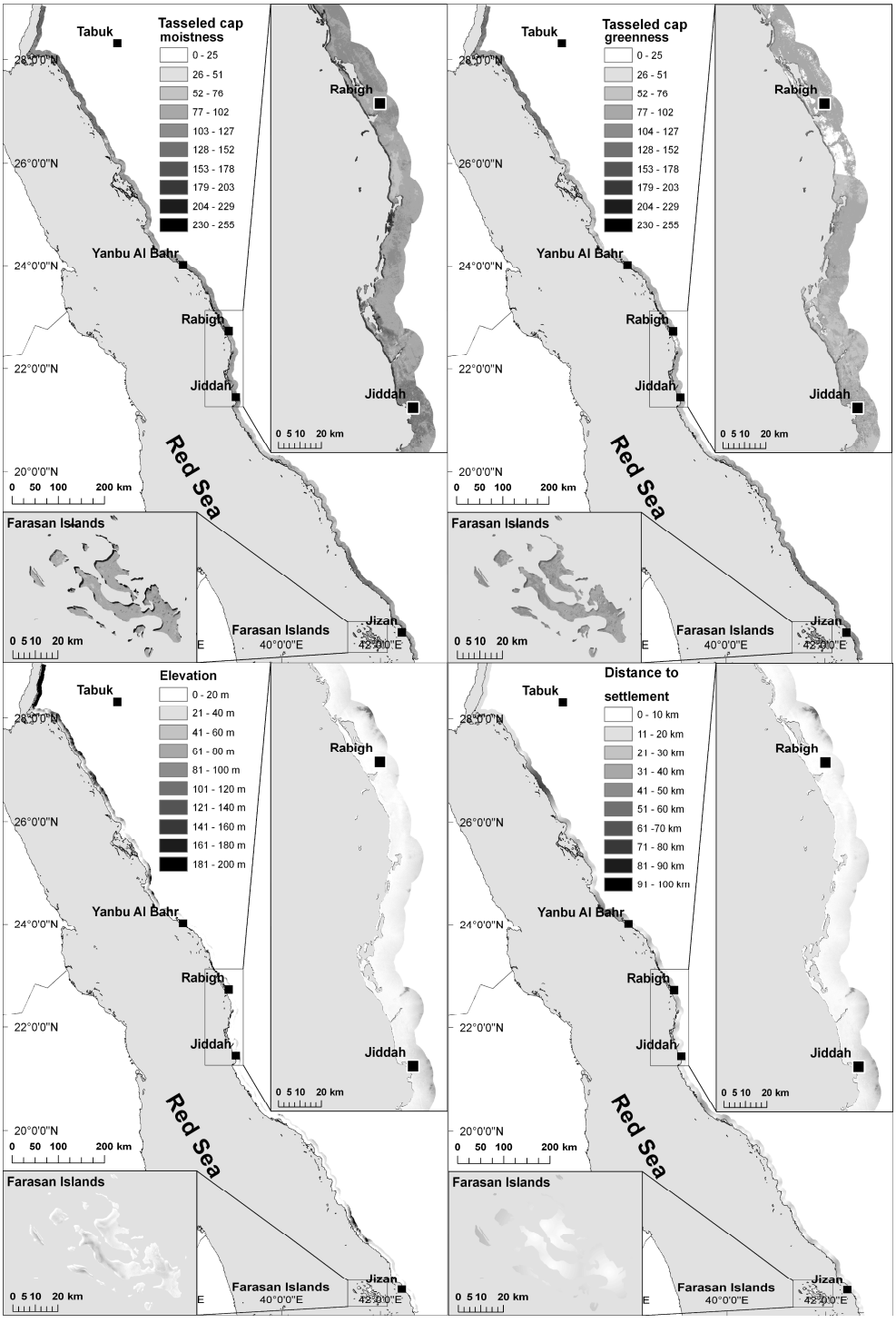


**Fig. 2.** Four *environmental variable maps used to model the Kentish plover distribution.*

***Species distribution modelling***

Generalised linear models (GLM) offer a simple and effective approach to modelling species' distributions (Brotons *et al*. 2004, Gibson *et al*. 2007, Mathys *et al*. 2006, López - López *et al*. 2007) and have been shown to be useful for shorebirds (Granadeiro *et al*. 2004). In order to make a GLM, the dataset must include presence and absence data. Since we were not able to collect definitive absence data for Kentish plovers, we generated a set of pseudo-absence data (Engler *et al*. 2004, Chefaoui & Lobo 2008, Gibson *et al*. 2007). Therefore, 766 points (an equal number to the total number of presences recorded) were generated randomly within a 250m buffer surrounding each of our sample routes where no Kentish plovers were found on either survey occasion. The complete data set of presences and pseudo-absences was then randomly split into two equal sized partitions: training data and validation data.

We used a GLM with a binomial error distribution to model the probability of presence in our training dataset as a function of the environmental variables. Following Pearce & Ferrier (2000) we decided to only use linear terms in our models to restrict the complexity of the fitted models. We used the program R 2.7.2 for all statistical analysis (R Core Development Team 2008). We expressed our model as a habitat suitability map using map algebra on our environmental variable maps and model coefficients.

We assessed the predictive accuracy of the distribution model by using our validation dataset to compute a Kappa statistic at every possible threshold value of the predicted habitat suitability map (Pearson 2007). We then plotted a receiver operating characteristic (ROC) curve to visualise the trade-off between the rate of omission errors (1-specificity) and commission errors (sensitivity) in our model across all threshold values. We then calculated the area under the curve (AUC) as a metric of model performance. The value of AUC can range from 0.5 for a model which performs no better than random to 1 for a model fits the data perfectly (Elith *et al*. 2006, Pearce & Ferrier 2000). Finally, we estimated the threshold value which maximises the Kappa statistic in order to subsequently reclassify our habitat suitability map to two levels: unsuitable habitat and suitable habitat (Liu *et al*. 2005).

***Estimating population size from the habitat suitability map***

First, we measured the area of habitat for Kentish plovers at each level of suitability by plotting a histogram of the final habitat suitability map. Our Kappa-maximising threshold, the probability of occurrence above which a habitat unit likely supports Kentish plovers, then allowed us to consider only the area of habitat predicted to be more suitable than this threshold.

Second, we estimated the density of Kentish plovers across our study area using the program DISTANCE 6.0 (Thomas *et al*. 2009). We modelled the probability of detecting a group of plovers as a function of perpendicular distance from the transect lines. We considered the robust models suggested by Buckland *et al*. (2001). These included the uniform key function with cosine and simple polynomial expansion series, the half normal key function with cosine and hermit polynomial expansion series, and the hazard rate key function with cosine and simple polynomial expansion series. We chose the best-fitting model, which was the half normal with cosine detection function, by using Akaike's Information Criterion (AIC), where the model with the smallest AIC indicates the best model.

## Results

We observed 1970 Kentish plovers in 766 groups during our surveys of 98 sample routes. The mean group size was 2.57±3.22 individuals. Kentish plovers were observed on at least one occasion on 69% of sample routes. We did not find Kentish plovers on 30 sample routes on either survey.

***Distribution model***

Kentish plovers were significantly more likely to be present in landscape units at lower elevations, with less green vegetation, greater soil moisture and in areas more distant from human settlements (Table 2). The final habitat suitability map shows varying levels of habitat suitability for Kentish plovers along the west coast of Saudi Arabia. Most of the suitable areas are concentrated from about 100 km south of Jiddah to Yanbu Al Bahr and near the city of Jizan. The suitable areas in the North are relatively small.

In the Farasan Islands, the most suitable habitat of Kentish plovers is located on the northern and eastern shores (Fig. 3)

**Table 2**. *Model of probability of the Kentish plover occurrence, logistic regression (GLM)*

| Response variable | Explanatory variable | Beta | *Z* | *P* |
|---|---|---|---|---|
| Kentish plover | Intercept | 9.597 | 9.837 | <0.001 |
| | Elevation | -0.230 | -8.257 | <0.001 |
| | Tasseled cap greenness | -0.016 | -3.833 | <0.001 |
| | Tasseled cap moistness | 0.010 | 3.331 | <0.001 |
| | Distance to settlement | -0.935 | -9.565 | <0.001 |
| Deviance = 1060.56, AIC = 824.4, n = 765 presences and pseudoabsences | | | | |

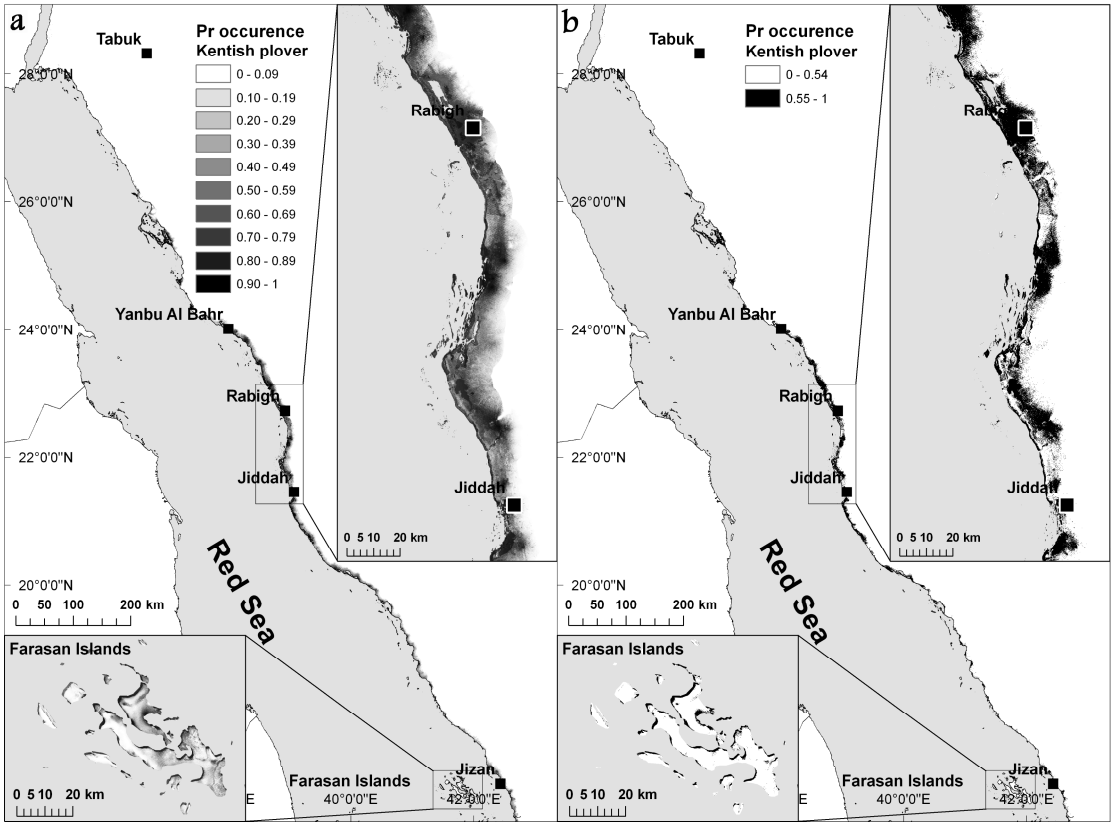


**Fig. 3.** *Final habitat suitability map. a) Absolute probability of occurrence of Kentish plover; b) Kentish plover present/absent. Absolute probability of occurrence map thresholded by the Kappa-maximising threshold.*

***Model validation***

The model performed well in predicting the Kentish plover presence when evaluated with an ROC plot (AUC mean= 0.796, SE= 0.016, Fig. 4). This suggests that in the final model, a cell predicted as suitable habitat, at any threshold of suitability, will be more suitable than a randomly selected cell in the study area at least 80% of the time.

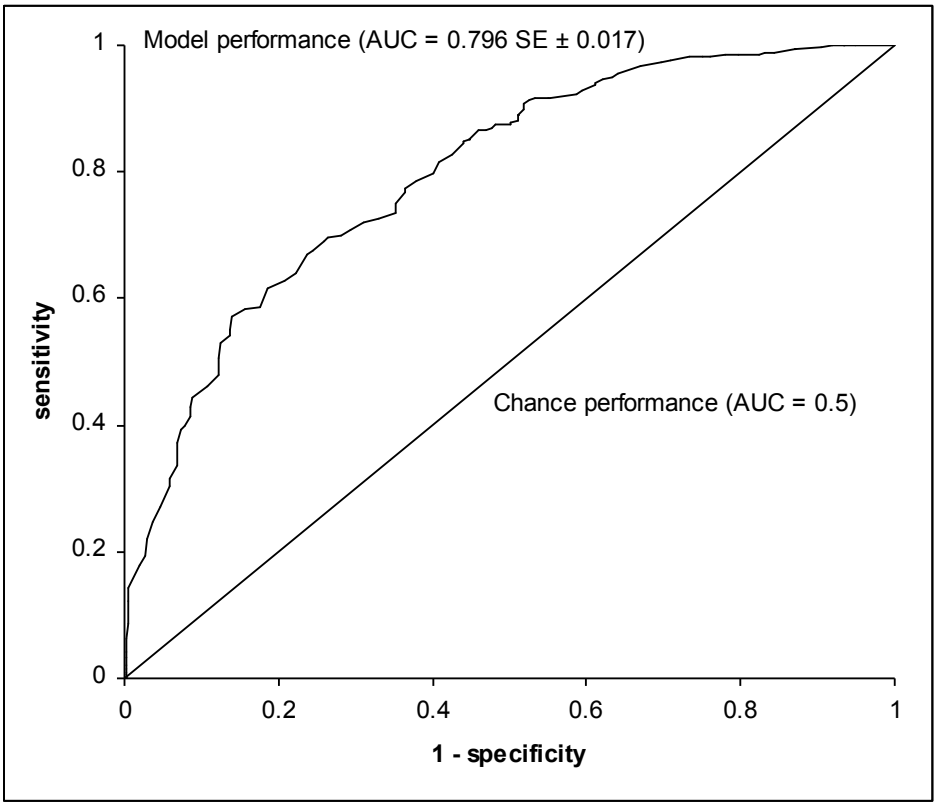


**Fig. 4.** *Receiver operating characteristic (ROC) plot of the Kentish plover distribution model performance relative to validation data. Sensitivity is the true positive fraction, and 1-specificity is the false-positive fraction for each unique threshold in the predicted distribution map. The diagonal line represents the model performance that would be expected by chance alone. The high AUC (0.796) of the model suggests that it has excellent power to discriminate between observed presence and absence.*

***Kentish plover population estimate***

The Kappa maximising threshold value of pr(occurrence) above which Kentish plovers will use the habitat was a probability of 0.55. Only cells that predicted a habitat suitability value greater than, or equal to, this threshold were considered to be suitable.

The total area of habitat more suitable than the threshold was 270 km2 (Fig. 5). The mean density of Kentish plovers across our study area was 36.87 ± 5.141individuals/km2. We therefore estimated the total population of Kentish plovers in our study area to be 9955±1388 individuals.

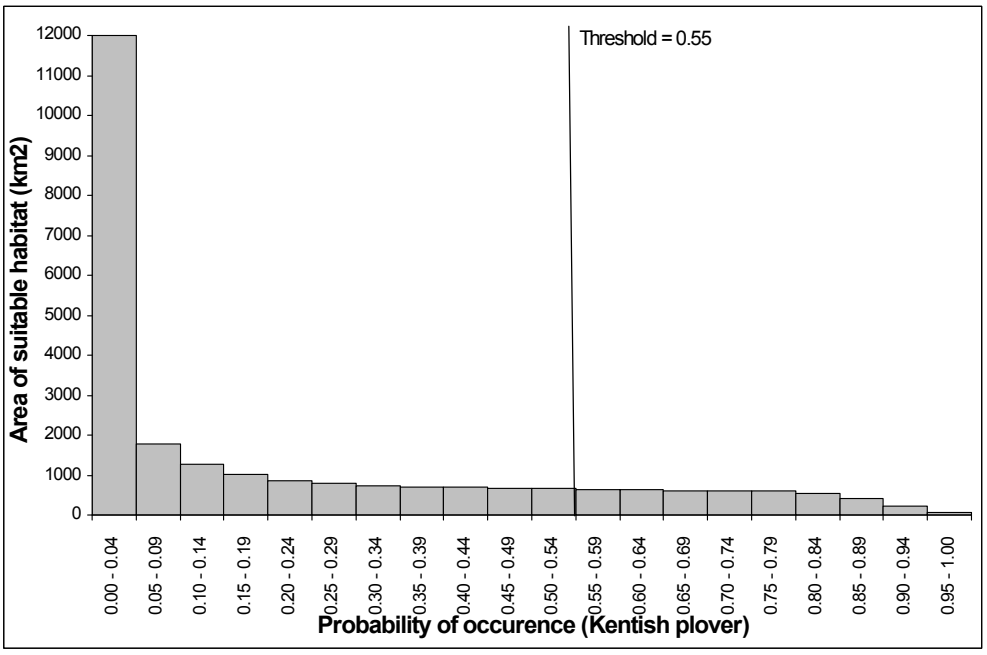


**Fig. 5.** *Histogram of area of suitable habitat in 0.05 bins of probability of occurrence of Kentish plovers. The vertical bar represents the 0.55 sensitivity-specificity threshold derived from the ROC curve. Kentish plovers will be absent from habitat less suitable than this threshold and present in the habitat more suitable than the threshold. The total area of the study region = 1078 km$^2$. However, the area of habitat more suitable than the threshold = 270 km$^2$.*

## Discussion

The results show that the Kentish plover prefers sites with low elevation, less vegetation, higher moistness and areas further away from human settlements. Distance to settlements probably has a negative significant influence because human activities and the density of predators such as dogs, cats and crows increase near settlements impact breeding and survival rates. Specifically these influences reduce incubation and brooding efforts and decrease foraging opportunities for adults and chicks (Lafferty 2000, Lafferty 2001, Ruhlen *et al*. 2003, Norte & Ramos 2004, Montalvo & Figuerola

2006). Several studies clearly indicated that the occurrence and distribution of the Kentish plovers were influenced by human activities. Montalvo and Figuerola (2006) found that Kentish plovers in Catalonia, Spain were disturbed by intensive tourist use of beaches and feral dogs and cats. Lamonte *et al*. (2006) also found that numbers of its close relative, snowy plover (*C. nivosus*), in Florida in both the breeding and non-breeding seasons were sensitive to human disturbance. On the coast of Eel River, California, human activity and predators significantly influenced the reproductive success of snowy plover (Colwell *et al*. 2005). The negative impact of human activities has been reported for many other plovers such as: piping plover (*C. melodus)* (Burger 1994), ringed plovers (*C. hiaticula)* (Liley and Sutherland 2007) and Malaysian plover (*C. peronii)* (Yasué and Dearden 2006).

The preference for open areas with less vegetation is probably related to providing visibility over a long distance for the detection of predator approaches (Page *et al*. 1983, Amat & Masero 2004). Snowy plover eggs and chicks probably are more cryptic in open sites such as saltmarshes because of their disruptive coloration (Page *et al*. 1983). Moreover, open areas allow the mobility required for ground running adults and precocial young. Plovers are known to find suitable habitats on open areas. For instance the majority of snowy plover breeding locations in the Caribbean and Bahamas are associated with salt flat habitat (Gorman & Haig 2002). At Atanasovsko Lake in Bulgaria, the decline in numbers of the Kentish plover breeding population was due to overgrowing of dikes by tall vegetation (Dalakchieva 2003). In the lower Laguna Madre region of Texas snowy plover nest survival decreased with increasing vegetation (Hood & Dinsmore 2007). Snowy plover nests in open sites in north-central Oklahoma had less predation risk (Winton *et al*. 2000).

It is likely that the observed preference for lower elevation and high moisture reflect the availability of food resources. Shorebird distributions are known to be strongly influenced by the distribution and abundance of food resources, and many studies have found a positive correlation between shorebird abundance and the abundance of their prey across large spatial scales (Colwell & Landrum 1993, Placyk & Harrington 2004, Ribeiro *et al*. 2004). Food abundance, predation pressure and indirect human disturbance were not included in our model because they could not be directly measured by remote sensing. Additionally, stochastic meta-population processes may mean that some potentially suitable habitat patches may not be occupied at certain times. The

collection of further field data in future studies will allow a fuller assessment of the adequacy of this model.

***Conservation implications and applications***

Based on our model and observations we recommend protection of the most suitable habitats along the western coast of Saudi Arabia, both from human activities and predation risk by selecting some areas and restricting human and terrestrial predators access with a fence. These areas should be large enough to provide good sites for foraging and nesting. We recommend the northern and eastern shores of the Farasan Islands to be one of the most important specific areas to given more protection by establishing new fenced areas. Each site should be at least 5×1 km. We also recommend establishing new areas about 20 km south of Jiddah, 10km north and south of the city of Jizan and 5 km south of Rabigh, each area should be at least 15×1 km.

In conclusion, it is necessary to identify environmental variables defining suitable habitat for species on a large spatial scale in order to underpin and evaluate conservation planning. We believe that our modelling approach can provide a foundation for conservation planning and long-term population monitoring of Kentish plovers and the other shorebirds in this region. We also believe that conservation of Kentish plover suitable habitat will not only protect this species but will benefit other shorebird species particularly those with similar habitat requirements. We also recommend that some areas with high habitat suitability to be identified for use in further protected area planning.

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# Chapter 6

# Conclusions and future directions

Monif AlRashidi

My PhD provided novel results that will have implications on two important fields of biology: breeding system evolution and conservation of wetland bird species. Specifically,

- I showed that harsh environments, particularly hot environments, have important implications for parental care evolution, since Kentish plover parents cooperated better by providing more biparental care and showed tighter coupling in their incubation behaviour during midday when temperatures were high, than during other parts of the day. I conclude that such a behavioural strategy is essential, since a single parent cannot protect the eggs and/or itself from overheating (Chapter 2).
- I tested the preceding proposition experimentally taking advantage of the natural variation in nest cover. My starting premise was that parents at shaded nests experience cooler temperatures. By experimentally manipulating nest cover I show that incubating parents do respond to the manipulation in the predicted way. At experimentally shaded nests the number of incubation changeovers decreased, whereas at uncovered nests the changeovers increased. I argue that this is largely because nest exposure in conjunction with extreme heat may favour tight coordination and cooperation between incubating Kentish plovers (Chapter 3).
- Using the findings from Chapter 2 & 3, I evaluated the role of the harsh environment on breeding ecology, and compared the behaviour of plovers in the Farasan Islands with that of other populations. I show that some features of this population (for example high site fidelity, high mate fidelity and a rarity of brood desertion) differ from that of the other plover populations. The precise reasons of these differences will require further analyses, although I argue they are largely due to the extreme hot environment, and/or life-history adaptations to island breeding (Chapter 4).
- Finally, I mapped suitable habitat and estimated the population size of Kentish plover along the poorly protected Red Sea coast of Saudi Arabia. I show that Kentish plover are most likely to occur in coastal habitat at low elevations, far from settlements, with high soil moisture and low vegetation cover. I recommend establishing new wetland protected areas on the west coast of Saudi

Arabia. I argue that when preparing conservation plans in data-poor areas, common species may act as useful proxies for wider biodiversity by allowing rapid selection of the most important wetland sites in a large region. I conclude that Kentish plovers could be used as a flagship species for designation of new protected areas and thus conservation of Kentish plover habitat will not only protect this species but will benefit other shorebird species particularly those with similar habitat requirements (Chapter 5). I anticipate that these results and the methodology I developed in the thesis will be used by the Saudi Wildlife Commission (SWC) to advance biodiversity conservation in Saudi Arabia.

## Future directions

The PhD projects have generated a number of promising lines of research that may be addressed by future research.

Firstly, from the perspective of evolutionary biology, new research is needed to establish experimentally the effects of the environments on parental care evolution in nature (McGraw et al. 2010). Preceding experiments were often carried out in the laboratories under well controlled environments, where the animals have limited choices to respond (Cantoni and Brown 1997). Only few experiments manipulated directly the environment and investigated the parental responses to the altered environment (Kosztolányi et al. 2003; Brown et al. 2010). To have a better understanding of parental care evolution, it is essential to have more and better manipulations, preferably in the natural environment of the animals.

Secondly, in the context of global environmental change and the biodiversity crisis, more research and conservation efforts are urgently required to inform conservation strategies to arrest global declines in biodiversity and the provision of ecosystem services. Some natural habitats are rapidly disappearing, and the pressures on the remaining habitats are increasing as a result of human activities (Groombridge and Jenkins 2002; Jeffries 2006). In spite of the hope that the rate of biodiversity loss will have slowed down by 2010, there is strong evidence to the contrary (Butchart et al. 2010).

Thirdly, in the specific context of breeding systems and conservation of birds in Saudi Arabia, my PhD has highlighted three interesting questions:

***1- How does the ambient environment influence incubation behaviour in different plover populations?***

Cross-population comparisons of a single species that breed in different habitats is a powerful approach to understand how ecological adaptation of a specific habitat influences behaviour and life history (Bennett & Owens 2002). Extending the analyses to closely-related species whilst controlling for the relatedness of populations and species can improve statistical power. The Kentish plover and its closely-related species (snowy plover *C. nivosus*, white-fronted plover *C. marginatus*, red-capped plover *C. ruficapillus* and Javan plover *C. javanicus*) have widespread geographic distributions; they breed on all continents except Antarctica (Küpper et al. 2009). Diurnal incubation in these species is mostly performed by the female. Female diurnal incubation appears to differ among Kentish plover populations (Rittinghaus 1961, Nakazawa 1979; Székely et al. 1994; Torre and Ballesteros, 1997; Kosztolányi & Székely 2002; Chapter 2) (Fig.1). This may be because males increase their nest attendance during high ambient temperatures, since females may not be able to incubate the eggs alone for long periods (Amat & Masero 2004; Chapter 2).

Little is known about the incubation behaviour of the closely related species of the Kentish plover. However, in the red-capped plover males exclusively incubate at night do not provide any incubation during daytime (Bywater 2009). The red-capped plover breeds in hot wetlands of Australia, and other factors such as conspicuousness of the males to predators (they wear a flame red cap) may explain the observed pattern in this closely related species. The variation in incubation routines provides an excellent opportunity to understand how extreme ambient temperatures (cold or hot), and other measurable environmental factors influence incubation routines across different populations; and how males and females cooperate to hatch their eggs.

Working out the effects of environment on parental behaviour is not trivial. Harsh temperature should promote cooperation, both parents should share incubation duties equally during periods with adverse temperature, therefore a quadratic relationship

between ambient temperature and nest attendance is predictable (i.e. increase of nest attendance when ambient temperature deviates from the optimum). Other ambient variables, social environments and life history may confound the influence of ambient temperature on biparental care, therefore controlling for their effect is required. For example, clutch volume may influence parental cooperation, so that more cooperation is expected with increasing clutch volume, because the probability of producing more chicks may stimulate parents to help each other. Egg-laying date may also affect parental cooperation: as the breeding season progresses, the chance of successful re-mating may become limited due to unsuitable weather conditions or food may become scarce, forcing parents to stay together and share parental duties. Finally, the incubation stage may also affect parental cooperation: more cooperation may be required as the incubation stage progresses, since the probability of hatching is high.

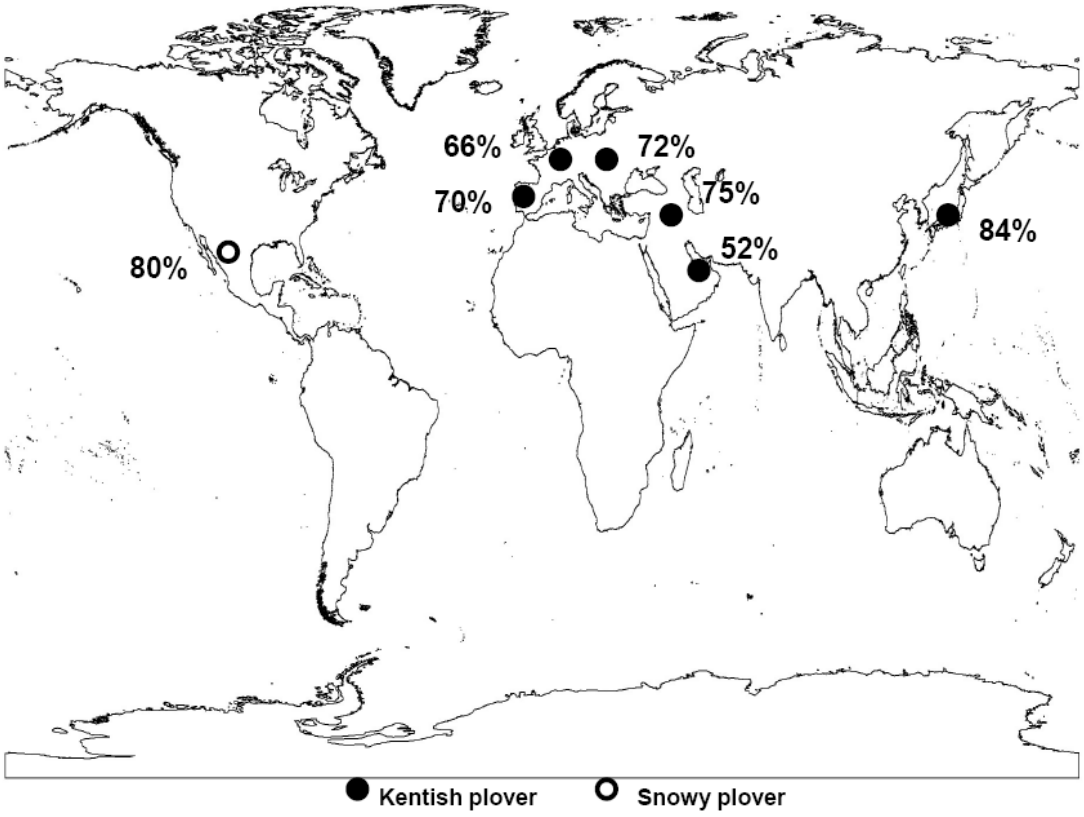


Fig.1 Female's diurnal incubation appears to differ among Kentish and snowy plover populations.

### *2- Estimating population size of birds using habitat suitability models*

Our habitat suitability modelling approach can be extended and integrated with distance sampling in order to estimate population sizes of bird species in Saudi Arabia and elsewhere, especially little-known species such as white-eyed Gull *Larus leucophthalmus*, an endemic species of the Red Sea (PERSGA/GEF 2003), and crab plover *Dromas ardeola* which nests only in islands of the Red Sea and the north-western Indian Ocean (De Marchi *et al*. 2006). A further extension to this approach is to consider a larger set of species, such as all wetland birds in the Red Sea coast, make and validate distribution models and use these models for systematic conservation planning to identify sites for protected areas.

### *3- Long-term monitoring breeding Kentish plover population in Farasan Islands*

The Farasan Islands offer an excellent opportunity to investigate the life-history of a Kentish plover population, and it is ideal for long-term monitoring and carrying out specific ecological research. Long-term monitoring of a single plover population will permit investigation of how the survival of adults and juveniles, sex ratio and mate availability influence parental care, and how the frequencies of these traits vary between generations. Additional benefits of a long-term monitoring population would be the ability to investigate how genetic basis influences nest-site selection. Investigating the heritability of nest-site selection may allow one to address whether chicks hatched from covered nests are, for instance, more likely to nest at covered sites, whereas chicks hatched from exposed nests may be more likely to nest at exposed sites. In addition, some of islands of Farasan Islands are inhabited and some of which are not. This gives an excellent opportunity to investigate the effect of human disturbance and introduced predators on Kentish plover population.

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